TEMPORAL AND SPATIAL VARIATION IN COMMUNITY DIVERSITY, RICHNESS, AND ABUNDANCE OF ICHTHYOPLANKTON IN COASTAL NEWFOUNDLAND OVER TWO DECADES

KELLY P. CARTER-LYNN

Temporal and Spatial Variation in Community Diversity, Richness, and Abundance of Ichthyoplankton in Coastal Newfoundland Over Two Decades

By

Kelly P. Carter-Lynn

Department of Biology and Ocean Sciences Centre
Memorial University of Newfoundland

A dissertation submitted to the Department of Biology in partial fulfillment of the requirements for the degree of Master of Science

September 2009

St. John's, Newfoundland

Abstract

I examine the patterns of variation in the larval fish community from coastal Newfoundland using data from 68 surveys conducted during the summer months between 1982 and 2002. I review the literature concerning changes in the adult fish community that have taken place, and then review the hypotheses about their possible causes. The principle debate surrounding the collapse of the Newfoundland groundfish deals with the relative roles of fishing pressure versus the potential influence of seawater temperature during the years following peak fishing pressure in the 1960's. I address whether differences in gear type (Bongo vs. Ring nets) might affect my ability to detect changes in the larval fish community as a result of selection loss or avoidance. Based on the results of statistical comparisons and on calculated catch ratios of < 1.6 I concluded that no consistent bias was present as a result of gear type and that the abundance data in this study are sufficiently comparable for use in larger temporal studies. I then contrast temporal changes in the larval community of three bays. Based on Multidimensional Scaling plots, Group Average Cluster Analysis and species abundance plots, I concluded that temperature (seasonal structure) plays a role in determining community composition of the larval fish studied, producing distinct larval assemblages at specific times of the year. I also concluded that below average water temperatures during the early 1990's affected the community composition of the larva; as cold-water species were unusually present during summer months. Additionally Analysis of Similarity showed that larval species abundance significantly decreased post 1992 and some non-commercial species showed smaller declines in abundance than those commercially targeted. Finally, I examine the scale

at which these changes have occurred, to determine whether large-scale temporal changes occur in species diversity or dominance, and whether changes correlate within and among the bays surrounding Newfoundland's Avalon Peninsula. Larval fish abundance displayed significant changes during the same time periods in all the bays examined in this study. However, further investigation is needed before conclusions can be made regarding how species composition differs in the bays surrounding the Avalon Peninsula.

Acknowledgements

I would like to thank my thesis committee P.V.R Snelgrove, P. Pepin and B. deYoung, for their contributions and support. I would also like to thank J.T. Anderson, I. Bradbury, E. Dalley, J. Dower, C. Fitzpatrick, S. Fraser, E. MacDonald, G. Maillet, R. Laprise, B. Oake, R. Penney, G. Redmond, P. Stead, T. Shears and the vessel crews from both Fisheries and Oceans Canada and Memorial University of Newfoundland and many others who have been involved in the collection and processing of ichthyoplankton samples over the last 20 years. This research was supported by National Science and Engineering Research Council of Canada Strategic and Discovery Grants to P. Snelgrove and to P. Pepin, as well as by Fisheries and Oceans Canada.

Table of Contents

List of Tables

List of Figures

I. Larval Fish Community Diversity

i. Introduction

Conservation and fisheries biologists have struggled for decades to characterize the factors that influence biological community structure and maintain diversity. These efforts were motivated by the intellectual, environmental, and economic gains that could be achieved by understanding communities in their natural state, as well as the desire of managers to ensure that decision making is based on a sound knowledge and understanding (Gauch, 1982; Cyr et al., 1992). This interest is heightened by increasing concerns over human impacts on natural communities and the physical environment. One of the best approaches to assess the severity or scale of environmental degradation is through long-term monitoring of biological communities, because some communities and species may be highly vulnerable to exploitation and habitat loss (Gauch, 1982; Magurran, 1988; Moser and Smith, 1993; Williamson, 1997), and can thereby serve as harbingers of broader change. Consequently, there is a need for consistency and cooperation among scientists in designing collection methods, analyzing data, and making inferences based on community studies (Orlóci, 1978; Moser and Smith, 1993; Sammons and Bettoli, 1998).

Of the different types of biodiversity (phylogenetic, morphological, genetic, and ecological), ecological, and more specifically species, diversity is the area most extensively studied (Williamson, 1997). Despite extensive efforts however, ecological diversity remains one of the most difficult forms of biodiversity to assess

quantitatively because of the problem of comparing or calibrating different measures and approaches. For example, differences in the sampling method used to collect data or natural fluctuations in species dominance and abundance (e.g., sardines vs. anchovies - Chavez et al., 2003) within biological communities make it difficult to identify what could be considered "normal" for a given community (Shackell and Frank, 2000). The majority of biodiversity research has therefore focused on species counts and related measures (Williamson, 1997), though even species counts are notoriously sensitive to sample size and effort (Magurran, 1988). Species counts, though flawed, are nonetheless an informative measure, and there is currently a surge of interest in marine biodiversity (e.g. Malakoff, 2003), in part to catalogue known species to assess better the number of species being lost to extirpation. It is the knowledge of how species interact with their environment, and the resulting shifts in species compositions, that will allow greater advances in biological conservation and in understanding variability in the nature of biological communities

Spatial and temporal patterns in biodiversity are cornerstones of ecology (Magurran, 1988; Legendre et al., 2002). On a global scale, latitudinal (e.g. Angel, 1997; Irigoien et al., 2004) and depth-dependent (Rex et al., 2001) diversity gradients have been described for many organisms (Huston, 1994; Williamson, 1997). Regional patterns (100s to 1000s of km), where evolutionary rather than ecological processes dominate, are termed gamma diversity patterns (Gray, 1997). Smaller-scale patterns (10s to 100s of km) involving multiple habitats or community boundaries are termed between-habitat or beta diversity. The latter illustrates the way in which organisms respond to

environmental heterogeneity and reflects the scale of patchiness (Huston, 1994) and represents the scale of diversity that will be considered in this study. The smallest diversity scale, known as alpha diversity, refers to the scale at which organisms are presumed to interact with each other and to compete for similar resources (Gray, 1997; Shackell and Frank, 2000), and reflects of the scales at which most samples are collected.

Ichthyoplankton surveys have multiple applications. They have been used extensively as a means of estimating fish biomass because these surveys are relatively comprehensive and fishery-independent (Morse, 1989; Moser and Smith, 1993). Larval fish are also more susceptible to collection than are adult fishes and, as a consequence, have produced higher estimates of species diversity when compared to surveys of juvenile or adult fishes (Shackell and Frank, 2000; Norberg, 2004 as cited in Govoni, 2005). Egg and larval surveys have also been used widely to try to understand population biology of individual species (e.g. Mukhina et al., 2003), community dynamics (e.g. Garrison et al., 2002), and the basic ecology of fishes (e.g. Claramunt et al., 2005). The focus of this study is ichthyoplankton community diversity in coastal Newfoundland, and the factors that contribute to variability in diversity in space and in time during a period when major changes occurred in the adult fish community (Taggart et al., 1994; Gomes et al., 1995). Diversity here is defined as the number of different species present in a community, while taking into account the proportion of community abundance that is accounted for by each species. The purpose of the following discussion is to review existing data describing known

associations between the physical environment, data collection methods, and larval fish assemblages.

ii. Evidence of Environmental and Physical Effects on Larval Fish Community Diversity

Larval dispersal plays a critical role in the survival of the early life stages of fish (Frank and Leggett, 1983; Pepin et al., 1995; Bradbury et al., 1999; Bradbury et al., 2000; Bradbury et al., 2003). Advective transport of ichthyoplankton influences abundance and distribution, and provides the mechanism that drives population retention or dispersal (Govoni, 2005). Smith and Suthers (1999) and Hinrichsen et al. (2003) provide clear evidence demonstrating the influence of advection on the structure of ichthyoplankton assemblages.

Bradbury et al. (1999) found that spawning location and timing in Atlantic cod may determine the roles that temperature and coastal circulation play with regard to distribution patterns and hatch success. Studies of larval fish assemblages in the Benguela Current have demonstrated that variation in upwelling events strongly affect, or may even control, assemblage composition and the abundance of component species (reviewed by Moser and Smith, 1993). Hare et al. (2002) suggested that transport by warm-core rings, Gulf Stream meanders, Gulf Stream filaments and mesoscale eddies off the north-eastern United States may control the larval supply to juvenile habitat and consequently affect the composition of ichthyoplankton assemblages in the slope sea region. These oceanographic features can influence the

timing and magnitude of recruitment to specific coastal areas in the Middle Atlantic Bight for different species that are transported across the shelf during their early life history.

Pepin et al. (1995) estimated that advection contributes from 12-75% of the daily variability in individual species abundances in Conception Bay, Newfoundland. These observations are in agreement with reports of adults spawning in consistent locales over time, presumably to take advantage of specific hydrographic phenomena (Frank and Leggett, 1983; Laprise and Pepin, 1995; Bradbury et al., 2000; Snelgrove et al., in prep.). Localized spawning by adult fish may result in larval retention in estuarine or coastal habitats that exhibit increased food concentrations of edible sizes, reduced predation rates, and optimal growth temperatures ("safe sites") (Frank and Leggett, 1983; Laprise and Pepin, 1995; Bradbury et al., 2000).

Numerous studies had demonstrated that interannual and seasonal differences in species composition and abundance are related to environmental variability with temperature fluctuations as the predominant driving factor (Morse, 1989; Laprise and Pepin, 1995; Pyper and Peterman, 1998). Laprise and Pepin (1995) also reported an order of magnitude lower egg and larval abundance in cold and less saline waters. Bradbury et al. (1999) found that Atlantic cod larvae that were spawned in the summer, rather than early spring, were an order of magnitude more abundant than larvae produced from spring spawning, despite much higher egg production in spring. They attributed reduced egg and larval dispersal in summer to decreased development

times in warmer waters relative to spring. Warmer water in summer decrease development times, allowing larvae to become strong swimmers at an earlier age and thus potentially reduces advective loss from inshore waters (see also Morse, 1989; McGovern and Olney, 1996; Pepin et al., 1997). Snelgrove et al. (in prep.) also suggested a strong association between water masses and larval fish species composition in Newfoundland waters.

In a study contrasting larval assemblages in two Leeuwin Current eddies, Muhling et al. (2007) found that larval fish assemblages varied significantly between the warm and cold water eddies, primarily as a result of differences in common species. Larval assemblages were more strongly structured with depth in the cold-core eddy and with mixed layer depth in the warm-core eddy. Sea surface temperature was the key variable differentiating larval fish assemblage structure between eddies. A study by Sassa et al. (2007) showed that larval assemblages corresponded closely to the positions of the Oyashio and Kuroshio Extension fronts, Oyahio cold-water mass, warm core rings, and streamers, however, there was also a seasonal component to the pattern of variation. Spawning location and advective transport were described as the underlying mechanism for these patterns.

An additional effect of spawning strategy is that larvae of pelagic spawners are more likely to be strongly associated with environmental cues than larvae of demersal spawners (Snelgrove et al. 2008), whereas demersal spawners are more clearly associated with spawning habitat than with hydrographic factors. Food availability

may be more ubiquitous early in the season (spring bloom) when demersal larvae are in their earliest stages of development, reducing the need for demersal larvae to associate with specific conditions or geographic areas (Sherman et al., 1984; Snelgrove et al., 2008.). In addition temperature may be less of an issue for demersally spawned eggs because eggs are not advected during development and larvae hatch at larger sizes and are therefore less susceptible to the effects of transport on their likelihood of survival (Thresher, 1984; Snelgrove et al., 2008).

iii. Problems in Evaluating Larval Fish Diversity

The well-known spatial heterogeneity exhibited by larval fish assemblages makes it difficult to sample these communities and obtain unbiased samples with low variability (Cyr et al., 1992; Pepin and Shears, 1997; Legendre et al., 2002; Pepin et al., 2005). Basing inferences about larval fish community dynamics on a literature in which sampling typically involves a few large samples confuses the issues even further (Cyr et al., 1992). It has been well established that sampling precision decreases in a particular region as the abundance of organisms and volume of water sampled decrease; however, the precision of estimated population density can be improved by increasing sample number or sample size (Downing et al., 1987; Cyr et al., 1992; Legendre et al., 2002; Pepin et al., 2005). Downing et al. (1987) and Helbig and Pepin (1998a, b) therefore advise researchers working in highly dynamic regions to increase the number of samples collected beyond requirements based on mean density and volume of water sampled alone. Quantitative estimates of sampling variability are necessary in order to make informed decisions as to the number of

samples required to accurately sample a given population or community (Downing et al., 1987).

As discussed by Overton and Rulifson (2007), the interpretation of abundance estimates for fish larvae may depend on the strengths and weaknesses of the collection gear. Differences among sampling gears is likely to affect estimates of the diversity, abundance and the size distribution of the population sampled (Sammons and Bettoli, 1998; Claramunt et al, 2005; Overton and Rulifson; 2007). Simultaneous sampling with gears that vary in type and size may also produce different diversity and abundance estimates (Gallagher and Conner, 1983; Cyr et al., 1992; Pepin and Shears, 1997; Claramunt et al., 2005; Pepin et al., 2005; Overton and Rulifson, 2007). Pepin and Shears (1997) showed that because Tucker trawls sample a larger volume of water than bongo nets, they also produce significantly higher estimates of species diversity for larval fish. They also found a significant day of year effect on species diversity, confirming temporal differences in larval fish community composition. These findings support those of McGowan and Fraundorf (1966) who observed greater species diversity and abundance of zooplankton when nets with greater mouth sizes were used. Larger nets such as Tucker trawls, which filter larger volumes of water, are also the superior gear choice for the collection of rare species because they exhibit reduced sampling variability (Pepin and Shears, 1997). Pepin et al. (2005) also point out that the vertical distribution of organisms in the water column can affect the accuracy of a given sampler. Vertical stratification of the water column can also complicate comparisons between gear types if the gears are deployed to different depths (Cada

and Loar, 1982).

Net avoidance by some taxa is a problem with all gear types; and increases as the length of the larva, and hence swimming ability, increases (Brander and Thompson, 1989; McGurk, 1992; Sammons and Bettoli, 1998). Net clogging (Hale et al., 1995; Isermann et al., 2002) and larval extrusion (of smaller individuals) can also occur; therefore mesh size is an important consideration in order to effectively sample individuals from a target population (Cada and Loar, 1982; Brander and Thompson, 1989; Morse, 1989). One final issue that complicates the measurement of larval diversity is catchability of larval fish under different light regimes (Gallagher and Conner, 1983; Morse, 1989; Brander and Thompson, 1989; Overton and Rulifson, 2007). Larvae of different species may avoid nets differentially as a function of available light; (Morse, 1989; Pepin and Shears, 1997) resulting in the possibility that the time of day the samples are collected may affect the observed community composition. Therefore as Overton and Rulifson (2007) point out, understanding the strengths and weaknesses of the gears used should direct the interpretation of the abundance estimates that the gears produce.

iv. Summary and Thesis Outline

It is clear that sampling larval fish in a physically dynamic environment such as coastal Newfoundland poses many challenges. Large-scale temperature variability within the region has been suggested as a possible contributor to declines in ground-fish abundance (Taggart et al., 1994; Gomes et al., 1995) in addition to over-exploitation of fish stocks (Taggart et al., 1994; Rose, 2003). The closure of the

Atlantic cod fishery punctuates the need to understand how environment and physical processes determine larval community composition. An initial step towards this goal is to determine whether consistent patterns exist in Newfoundland coastal areas, and to take advantage of historical ichthyoplankton data to infer how patterns in larval abundance and composition have changed over time during a period when environmental variability and fishing-induced changes in community structure were pronounced. This approach provides a complementary approach to analyses of adult fish communities (Taggart et al. 1994, Gomes et al. 1995), because larval surveys do not selectively target commercial species, thereby potentially revealing patterns in a broader range of species.

The available historical data on icthyoplankton in coastal Newfoundland have been collected with different gear types and the goal of Chapter 2 is to describe how these gears are biased and how the different data sets produced by these sampling efforts can be compared. These data sets were collected for multiple purposes at the time they were assembled and, while standardized sampling would have been ideal, *these data sets represent the only historical record available on larval fishes during a critical time in the Newfoundland fishery* in terms of changing adult abundances and composition in coastal Newfoundland (Taggart et al., 1994; Gomes et al., 1995). Larval samples offer important insight because they are not biased towards commercial taxa and encompass a wide range of ecological guilds. Establishing a mechanism to compare these data sets is particularly important in terms of understanding how larval composition has changed over time and space, and the data

presented here offer the only means of making such comparisons which have significant potential for understanding long-term changes in this ecosystem. Having identified the potential biases of sampling gear in Chapter 2, I then examine temporal changes in icthyoplankton in Newfoundland embayments at multiple time scales in Chapter 3. First, I determine how patterns in diversity, abundance and composition change seasonally from the spring to late summer, which encompasses the times of year when larval sampling was conducted. I then use that information on seasonal change to interpret how patterns have changed based on the multiple studies that were conducted from 1982 through 2002, and attempt to link those changes to environmental conditions. In Chapter 4, I examine how larval fish composition and abundance compare among bays, in order to address whether there are differences in composition at larger spatial scales (100s of km) that can be detected in the context of high patchiness and within-bay variability. Collectively these chapters address the question of whether clear and consistent patterns can be identified in terms of broad spatial areas (100's of km) and long time periods (decades) amid strong local spatial and seasonal signals, and how these data can be used to understand how fishes in Newfoundland have changed over the last few decades.

v. Literature Cited

Angel, M.V. (1997) Marine Biodiversity: Patterns and Processes. Edited by R.F.G. Ormond, J.D. Gage and M.V. Angel. Cambridge University Press. New York.

Bradbury, I.R., P.V.R. Snelgrove and S. Fraser (1999) Transport and development of cod eggs and larvae in Placentia Bay (3Ps) Newfoundland, 1997-1998. Canadian Stock Assessment Secretariat. Research Document 99/71. Department of Fisheries and Oceans, Canada.

Bradbury, I.R., G.L. Lawson, D. Robichaud, G.A. Rose and P.V.R. Snelgrove. (2000) Success and Failure of Atlantic cod, *Gadus morhua*: a case study from coastal Newfoundland. Canadian Stock Assessment Secretariat. Research Document 2000/022. Department of Fisheries and Oceans, Canada.

Bradbury, I.R., P.V.R. Snelgrove and P. Pepin (2003) Passive and active behavioural contributions to patchiness and spatial pattern during the early life history of marine fishes. Marine Ecology Progress Series 257: 233-245.

Brander, K. and A.B. Thompson (1989) Diel differences in avoidance of three vertical profile sampling gears by herring larvae. Journal of Plankton Research. 11: 775-784.

Cada, G.F. and J.M. Loar (1982) Relative effectiveness of two ichthyoplankton sampling techniques. Canadian Journal of Fisheries and Aquatic Sciences. 39: 811-814.

Chavez, F.P., J. Ryan, S.E. Lluch-Cota and M. Niquen C. (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science. 299: 217-221.

Claramunt, R.M., D.E. Shoup and D.H. Wahl (2005) Comparison of push nets and tow nets for sampling larval fish: Implications for assessing littoral habitat utilization. North American Journal of Fisheries Management. 25: 86-92.

Cyr, H., J.A. Downing, S. Lalonde, S.B. Baines and M.L. Pace (1992) Sampling larval fish populations: choice of sample number and size. Transactions of the American Fisheries Society. 121: 356-368.

Downing, J.A., M. Pérusse and Y. Frenette (1987) Effect of interreplicate variance on zooplankton sampling design and data analysis. Limnology and Oceanography.32: 673-680.

Frank, K.T. and W.C. Leggett (1983) Multispecies larval fish associations: accident or adaptation? Canadian Journal of Fisheries and Aquatic Sciences. 40:754-762.

Gallagher,R.P. and J.V. Conner (1983) Comparison of two ichthyoplankton sampling gears with notes on the microdistribution of fish larvae in a large river. Transactions of the American Fisheries Society. 112: 280-285.

Garrison, L.P., W. Michaels, J.S. Link and M.J. Fogarty (2002) Spatial distribution and overlap between ichthyoplankton and pelagic fish and squids on the southern flank of Georges Bank. Fisheries Oceanography. 11: 267-285.

Gauch, H.G. Jr. (1982) Multivariate analysis in community ecology. Eds. E. Beck, H.J. Birks and H.E.F. Connor. Cambridge University Press, Cambridge.

Gomes, M.C., R.L. Haedrich and M.G. Villagarcia (1995) Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991. Fisheries Oceanography. 4: 85-101.

Govoni, J.J. (2005) Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. Scientia Marina. 69 (Suppl. 1): 125-137.

Gray, J.S. (1997) Gradients in marine biodiversity. In: Marine biodiversity patterns and processes. Eds. R.F.G. Ormond, J.D. Gage and M.V. Angel. Cambridge University Press, Cambridge. pp. 1-17.

Hale, R.S., G.L. Buynak and J.R. Jackson (1995) Catch comparisons of surface sampling methods for age-0 gizzard and threadfin shad. North American Journal of Fisheries Management.15: 862-870.

Hare, J.A., M.P. Fahay and R.K. Cowen (2001) Springtime ichthyoplankton of the slope region off the north-eastern United States of America: larval assemblages, relation to hydrography and implications for larval transport. Fisheries Oceanography. 10: 164-192.

Helbig, J.A., and P. Pepin (1998a) Partitioning the influence of physical processes on the estimation of ichthyoplankton mortality rates I. Theory. Canadian Journal of Fisheries and Aquatic Sciences 55: 2189-2205.

Helbig, J.A., and P. Pepin (1998b) Partitioning the influence of physical processes on the estimation of ichthyoplankton mortality rates II. Application to simulated and field data.Canadian Journal of Fisheries and Aquatic Sciences 55: 2206-2220.

Hinrichsen, H-H., A. Lehmann, C. Möllmann and J.O. Schmidt (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography. 12: 425-433.

Huston, M.A. (1994) Biological diversity the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Irigoien, X., J. Huisman and R.P.Harris (2004) Global biodiversity patterns of marine phytoplankton and zooplankton. Nature. 429: 863-867.

Isermann, D.A., P.A. Hanchin and D.W. Willis (2002) Comparison of two mesh sizes for collecting larval yellow perch in surface trawls. North American Journal of Fisheries Management. 22: 585-589.

Laprise, R. and P. Pepin (1995) Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. Marine Ecology Progress Series. 122: 73-92.

Legendre, P., M.R.T. Dale, M-J. Fortin, J.Gurevitch, M. Hohn and D. Myers (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography. 25: 601-615.

Magurran, A.E. (1988) Ecological diversity and its measurement. Princeton University Press, New Jersey.

Malakoff, D. (2003) Scientists Counting on Census to Reveal Marine Biodiversity. Science. 302: 773.

McGovern, J.C. and J.E. Olney (1996) Factors affecting survival of early life stages and subsequent recruitment of striped bass on the Pamunkey River, Virginia. Canadian Journal of Fisheries and Aquatic Sciences. 53: 1713-1726.

McGowan, J.A. and V.J. Fraundorf (1966) The relationship between size of net used and estimates of zooplankton diversity. Limnology and Oceanography. 11: 456-469.

McGurk, M.D. (1992) Avoidance of towed nets by herring larvae: a model of night-day catch ratios based on larval length, net speed and mesh width. Journal of Plankton Research. 14: 173-182.

Morse, W.W. (1989) Catchability, growth, and mortality of larval fishes. Fishery Bulletin. 87: 417-446.

Moser, H.G. and P.E. Smith (1993) Larval fish assemblages and oceanic boundaries. Bulletin of Marine Science. 53: 283-289.

Muhling, B.A., L.E. Beckley and M.P. Olivar (2007) Ichthyoplankton assemblage structure in two meso-scale Leeuwin Current eddies, eastern Indian Ocean. Deep Sea Research Part II: Tropical Studies in Oceanography. 54: 1113-1128.

Mukhina, N.V., C.T. Marshall and N.A. Yaragina (2003) Tracking the signal in year-class strength of northeast Arctic cod through multiple survey estimates of egg, larval and juvenile abundance. Journal of Sea Research. 50: 57-75.

Orlóci, L. (1978) Multivariate analysis in vegetation research. 2nd ed. Junk, The Hague. pp. 451.

Overton, A.S. and R.A. Rulifson (2007) Evaluation of plankton surface pushnets and oblique tows for comparing the catch of diadromous larval fish. Fisheries Research. 86: 99-104.

Pepin, P., J.A. Helbig, R. Laprise, E. Colbourne and T.H. Shears (1995) Variations in the contribution of transport to changes in planktonic animal abundance: a study of the flux of fish larvae in Conception Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences. 52:1475-1486.

Pepin, P. and T.H. Shears (1997) Variability and capture efficiency of bongo and tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. Canadian Journal of Fisheries and Aquatic Sciences. 54: 765-773.

Pepin, P., D.C. Orr and J.T. Anderson (1997) Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences. 54(Suppl. 1): 2-10.

Pepin, P., P.V.R. Snelgrove and K.P. Carter (2005) Accuracy and precision of the continuous underway fish egg sampler (CUFES) and bongo nets: a comparison of three species of temperate fish. Fisheries Oceanography. 14: 432-447.

Pyper, B.J. and R.M. Peterman (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data. Canadian Journal of Fisheries and Aquatic Sciences. 55: 2127-2140.

Rex, M.A., C.T. Stuart and R.J. Etter (2001) Do deep-sea nematodes show a positive latitudinal gradient of species diversity? The potential role of depth. Marine Ecology Progress Series. 210: 297-298.

Rose, G (2003) Fisheries Resources and Science in Newfoundland and Labrador: An Independent Assessment. Royal Commission on Renewing and Strengthening our Place in Canada. 84 pp.

Sammons, S.M. and P.W. Bettoli (1998) Larval sampling as a fisheries management tool: early detection of year-class strength. North American Journal of Fisheries Management. 18: 137-143.

Sassa, C., K. Kawaguchi and K. Taki (2007) Larval mesopelagic fish assemblages in the Kuroshio-Oyashio transition region of the western North Pacific. Marine Biology. 150: 1403-1415.

Shackell, N.L. and K.T. Frank (2000) Larval fish diversity on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences. 57: 1747-1760.

Sherman, K., Smith, W., Morse, W., Berman, M., Green, J., and Ejsymont, L. 1984. Spawning strategies of fisheries in relation to circulation, phytoplankton production and pulses in zooplankton off the northeastern United States. Marine Ecology Progress Series. 18:1-19.

Smith, K.S. and I.M. Suthers (1999) Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf. Marine Ecology Progress Series. 176: 49-62.

Snelgrove, P.V.R., S. Fraser and I.R. Bradbury (in prep.) Spatial pattern in ichthyoplankton in Placentia Bay, Newfoundland and the roles of spawning strategy and advection. Submitted.

Snelgrove, P.V.R., I.R. Bradbury and S. Fraser (2008) Temporal variation in fish egg and larval production by pelagic and demersal spawners in a large Newfoundland coastal embayment. Canadian Journal of Fisheries and Aquatic Sciences. 65, 159-175.

Taggart, C. T., J. Anderson, C. Bishop, E. Colbourne, J. Hutchings, G. Lilly, J. Morgan, E. Murphy, R. Myers, G. Rose, and P. Shelton (1994) Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Marine Science Symposia 198: 140-157.

Thresher, R.E. (1984) Reproduction in reef fishes. T.F.H. Publications, Neptune City, New Jersey.

Williamson, M. (1997) Marine biodiversity in its global context. In: Marine biodiversity patterns and processes. Eds. R.F.G. Ormond, J.D. Gage and M.V. Angel. Cambridge University Press, Cambridge. pp. 1-17.

Table 1-1: **Summary of Coastal Newfoundland Ichthyoplankton Data**

Sampling Location	Sampling Date	Gear Type Used
Trinity Bay	May – October 1982	Bongo Net 333 µm mesh
Trinity Bay	May – October 1983	Bongo Net 333 µm mesh
Trinity Bay	May – October 1984	Bongo Net 333 µm mesh
Conception Bay	May-August 1985	Ring Net 165 µm mesh
Trinity Bay	May – October 1985	Bongo Net 333 µm mesh
Conception Bay	June - September 1986	Ring Net 165 µm mesh
Trinity Bay	May-October 1986	Bongo Net 333 µm mesh
Conception Bay	June/July 1990 September/October 1990	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Conception Bay	July 1991	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Conception Bay	July- September 1992	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Conception Bay	June 1993 July 1993 September 1993	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Conception Bay	July/August 1994 July 1994 July/August 1994 August 1994	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes

Table 1-1(cont.): **Summary of Coastal Newfoundland Ichthyoplankton Data**

Sampling Location	Sampling Date	Gear Type Used
Conception Bay	July/August 1994	Bongo Net 333 µm mesh
Conception Bay, Bonavista Bay & Trinity Bay	July/August 1997	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes & Bongo Net 333 µm mesh
Placentia Bay	April-June 1997, August & October 1997	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Conception Bay	July/August 1998	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes & Bongo Net 333 µm mesh
Placentia Bay	April, June, August & September 1998	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Placentia Bay	April, June, August 1999	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes
Trinity Bay	July 2000	Tucker Trawl 2x2 m 1000, 570, 333 µm mesh sizes & Bongo Net 333 µm mesh
Trinity Bay	May 2001	Bongo Net 505 µm mesh
Trinity Bay	August 2001	Bongo Net 333 µm mesh
Trinity Bay	May 2002	Bongo Net 505 µm mesh

Co-authorship Statement

Chapters 2, 3 and 4 are manuscripts in preparation for submission to the Fishery Bulletin, Canadian Journal of Fisheries and Aquatic Sciences and Canadian Journal of Zoology respectively. These manuscripts will be co-authored with Paul Snelgrove and Pierre Pepin, however, in all instances I was the principle contributor to project design, implementation, analysis of data and manuscript preparation.

II. Variability in Estimates of Shannon-Wiener Diversity, Species Richness and Abundance of Ichthyoplankton Collected in Coastal Newfoundland Using Tucker Trawls, Bongo Nets and Ring Nets

i. Introduction

In recent years, there has been increasing interest in utilizing historical data sets to improve our ability to assess long-term fluctuations in abundance and diversity of marine organisms. Historical data such as the CalCOFI time series and annual ichthyoplankton surveys by the National Oceanic and Atmospheric Administration's (NOAA) Alaska Fisheries Science Centre (AFSC) provide the opportunity to examine temporal and spatial patterns in larval fish abundance during periods when significant changes have been observed in adult populations. For example, Doyle et al. (2002) used historical ichthyoplankton data to provide new information on the spawning strategy and early life history of capelin (*Mallotus villosus*). Historical data can also be used in egg and larval production models to aid in assessing abundances of adult populations that are difficult to evaluate using traditional methods, or for adult populations where trawl samples are inaccurate or unreliable (Pepin et al., 2005). Nonetheless, the use of historical data can create challenges. For example, as old technologies are abandoned in favour of newer methods, it is important to intercalibrate data collected using different methodologies in order to assemble a long temporal history (Ohman and Lavaniegos, 2002). In addition, data may be collected for a variety of reasons, other than maintaining a time series, and sampling methodologies therefore may vary to suit specific applications.

Since the early 1980's there have been numerous ichthyoplankton surveys in coastal Newfoundland. Most have utilized one of three gear types: Tucker trawls, bongo nets, and ring nets. Pepin and Shears (1997) examined sampling variability and relative capture efficiency of Tucker trawls and bongo nets for ichthyoplankton, and determined that Tucker trawls yield higher estimates of community diversity. This difference is likely because Tucker trawls are more effective at sampling rare species (Pepin and Shears, 1997). Comparisons of Tucker trawl and ring net samples from south-western Nova Scotia showed that the ring nets effectively captured larvae sized <10 mm but ring nets underestimated numbers of larvae >10 mm as well as juvenile cod compared with Tucker trawl estimates (Suthers and Frank, 1989). However, these comparisons were for a 405 μm mesh ring net and 1600 μm mesh Tucker trawl. Therefore it is not surprising that the Tucker trawl underestimated the number of smaller larvae present as a result of the coarser mesh size. Following is a review of some relevant studies describing known biases in larval estimates produced using ring and bongo nets. These studies and others indicate that Tucker trawls will yield higher estimates of abundance and greater estimates of diversity for larval fish than will bongo or ring nets.

Johnson and Morse (1994) suggest that the two most important factors of uncertainty in abundance estimates of larval fish collected with towed nets are escapement and extrusion. In their study comparing bongo nets fitted with 333 and 505 μm mesh, they assumed that net avoidance was constant for both nets (see also Somerton and Kobayashi, 1989) and concluded that although bias would occur as a result of differential extrusion, this bias may be minor for comparisons between studies where larvae were collected

using different mesh sizes. Similarly, Taggart and Leggett (1984) compared the efficiency of a large volume plankton pump fitted with an 80 μm mesh cod end to a cylinder cone standard net fitted with 153 μm mesh during two years of their three-year study. As support that these mesh sizes could be intercalibrated these authors cite Fortier and Leggett (1983), who showed no significant differences in capture efficiency of capelin and herring larvae between a standard ring net fitted with 80 μm mesh and bongo nets fitted with 151 μm mesh. Net mouth diameter has also been suggested to affect the catchability of some types of zooplankton (Brinton and Townsend, 1981). McGowan and Fraundrof (1966) found no significant difference in euphausiid catches for different net types with similar mouth size; euphausiid swimming ability is likely comparable to that of larval fish, and therefore it is expected that larvae would show similar patterns of avoidance. Clupeid larvae sized 5-10 mm also show greater avoidance behaviour when confronted with a low volume pump (7.6 cm intake diameter) than larvae collected with a towed net (0.5 m mouth diameter) (Cada and Loar, 1982). These differences were not observed when sampling at night and were therefore concluded to be the result of visual not tactile stimuli.

Ring nets and bongo nets have been compared by several authors interested in the relative catchability of zooplankton (Brinton and Townsend, 1981; Ohman and Smith, 1995; Ohman and Lavaniegos, 2002; Rebstock, 2002). However, fewer comparative studies that target ichthyoplankton are available (Hewitt, 1980; Smith, unpublished in Brinton and Townsend, 1981; Fortier and Leggett, 1983; Suthers and Frank, 1989). Ohman and Lavaniegos (2002) reported that the only consistent differences in zooplankton species

between 1-m diameter ring nets and bongo nets were greater abundances of salps in bongo nets and higher species diversity of hyperiid amphipods in ring nets when larger numbers of individuals were enumerated. Smith (unpublished, cited in Brinton and Townsend, 1981) found that bongo nets collected significantly more anchovy larvae > 12 mm in length compared with ring nets. Larvae greater than 12 mm presumably were able to actively avoid the ring net by detecting the pressure wave created by the net and bridle. This analysis, combined with work done by Brinton and Townsend (1981), led to the adoption of bongo nets as the standard sampling method for CalCOFI plankton surveys, which had previously used a 1-m ring net as the standard (Brinton and Townsend, 1981).

Collectively, these studies clearly demonstrate that abundance and diversity estimates for larval fish produced by sampling gears that differ in mesh size, mouth diameter, and tow profile will each have their own inherent biases. Nonetheless, all of these approaches are considered effective (though selective, and therefore internally biased) methods for obtaining estimates of diversity and abundance of larval fish. Given that comparisons between different studies can often greatly extend the utility of individual data sets and sampling approaches, there is much to be gained by determining whether these different sampling efforts can be combined to address questions that cannot be addressed in any other way. Of particular importance is whether there is variability in the data that can be attributed to major changes in larval fish communities and separated from biases that are introduced into the data as a result of gear differences.

With the exception of the pump/ring net study by Taggart and Leggett (1984) and the

bongo net / Tucker trawl comparison of Pepin and Shears (1997) and a recent comparison of bongo nets and the Continuous Underway Fish Egg Sampler (Pepin et al., 2005), there are no gear calibration studies specific to ichthyoplankton communities in coastal Newfoundland. Given that much of the historical data has utilized either ring nets or bongo nets, the catalogue of ichthyoplankton data for the region contains a mismatch of sampling techniques that can only be compared if bias issues are carefully addressed. The best opportunity to address such biases is to compare concurrent studies that utilized different gears types; The overall objective is to assess ichthyoplankton data collected during the summers of 1985 and 1986 using bongo and ring nets to determine whether estimates of abundance, diversity, and species richness of ichthyoplankton in coastal Newfoundland obtained by the two gear types are comparable and to determine whether a consistent intercalibration factor can be developed for the two gear types.

ii. Methods

Data Collection

The data were collected in one of two adjacent Newfoundland embayments; Trinity Bay or Conception Bay (Figure 2-1). Trinity Bay is located on the northeast coast of Newfoundland and measures approximately 100 km long by 30 km wide. The bay reaches a maximum depth of 630 m in a deep trench that is located near the center of the bay (Pepin et al., 2005). A sill at the mouth of the bay has a maximum depth of 240 m. Wind forcing has a major effect on the stratification and circulation of both bays (Yao, 1986; Davidson et al., 2001). During the summer periods, when samples were collected, southwesterly offshore winds predominate and can create upwelling areas on the western

side of the bay (Pepin et al., 2005). Conception Bay, which is immediately east of Trinity Bay, is slightly smaller, at approximately 50 km long by 25 km wide, with a maximum depth of roughly 300 m. A sill at the mouth of the bay has a maximum depth of 150 m. Like Trinity Bay, Conception Bay is susceptible to wind forcing on short time scales (Pepin et al., 1995; Davidson et al., 2001). Specific analysis of data on environmentally-driven water mass variation was not undertaken in this study; however, other studies dealing with this question are presented in the Discussion.

Data from Trinity Bay were collected using a 61 cm bongo net (net side unspecified) fitted with 333 μm mesh Nitex. Data from Conception Bay were collected using a 50-cm ring net fitted with 165 μm mesh. Bongo net samples consisted of an oblique tow of approximately 15 min at a tow speed of approximately 2-3 knots. Bongo nets were lowered to a depth approximately 5-10 m from the sea floor or to a maximum depth of 200 m in deep areas. Ring nets were towed horizontally for approximately 15 min at a tow speed of ~ 2-3 knots at a depth of 7 m. For both samplers, volume filtered was estimated using a General Oceanics flowmeter.

Data used in this study were collected during the summers (June-Aug) of 1985 and 1986 (Figure 2-1). During the summer of 1985, 44 stations from Trinity Bay and 60 stations from Conception Bay were sampled in the month of June. During July, 55 stations from Trinity Bay and 83 stations from Conception Bay were sampled. Throughout the month of August, 57 stations from Trinity Bay and 47 stations from Conception Bay were sampled. Similarly, in June 1986, 57 stations were sampled in Trinity Bay and 20 stations

were sampled in Conception Bay. During July and August 1986, 54 and 57 stations were sampled respectively from Trinity Bay while 20 and 14 stations were sampled in Conception Bay. The two bays were compared by analyzing the samples by month; samples from Conception Bay were collected using ring nets and samples from Trinity Bay were collected using bongo nets. By pairing the samples by month, the variability associated with seasonality is minimized (seasonality data is presented for nearby Placentia Bay in Chapter 3). Spatial differences (i.e. within and between bays) in the populations being sampled are expected to contribute to overall variance, however, the largest and most consistent difference between samples is expected to result from differences in gear.

On deck, nets were washed and samples were preserved in 2% buffered formaldehyde. In the laboratory ichthyoplankton were sorted and identified to the lowest taxonomic level possible from each sample (for bongo nets one side was chosen at random). Between 0-11% of counts were produced from sub-samples (average < 2%); most sub-sampling was for capelin (*Mallotus villosus*), which was sometimes extremely abundant. Sub-sampling of an individual taxon used either a beaker technique or a Folsom splitter (van Guelpen et al., 1982) for samples in which numbers of a single species exceeded 200 individuals. Based on the studies of van Guelpen et al. (1982) and Sell and Evans (1982) the coefficient of variation (CV) for these sub-sampling methods is assumed to be 10-20 %. Abundance (number per 1000 metre^3) of each taxon was calculated for each sample and corrected for sub-sampling.

Data Analysis

Shannon-Wiener diversity (H), species richness (SR), abundance (larvae/1000 m^3) and water volume filtered (m^3) were computed at each station for 12 cruises (6 with bongo nets, 6 with ring nets) that took place in June-Aug 1985 and 1986. All statistical analyses were based on the comparison of each metric between gear types on a month-by-month basis. Shannon-Wiener diversity index (H) was computed for each sample using the formula:

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where H is the diversity in s species, s is the number of species present in the sample, p_i is the proportion of species i in the sample (n_i/n), and $\sum p_i = 1$. An estimate of H is therefore,

$$h = -\sum_{i=1}^{s} (n_i / n) \ln(n_i / n) \qquad (2)$$

given a random sample of n (total number of individuals in the sample from all species) observations from data in the s species i (1, 2, . . ., s) with probabilities p_i (1, 2, . . ., s), where h and H fall between zero and ln s (Hutcheson, 1970).

For each cruise, an overall estimate of the mean and variance (s^2) for Shannon-Wiener diversity (h), species richness (SR), abundance (larvae/1000 m^3) and volume filtered (m^3) were calculated. Hartley's (1950) F_{max} – test tested homogeneity of variance (s^2)

for each of the six comparisons (Sokal and Rohlf, 2000).

$$F_{max} = s^2_{max} / s^2_{min} \qquad (3)$$

Data found to have homogeneous variances on non-transformed or $\log_{10}$ transformed data were compared using *t*-tests (Hutcheson, 1970). In instances where transformation could not correct the problem of heterogeneous variance, a Mann-Whitney U-test for two independent means was applied to the data. Comparisons that showed no significant difference at $\alpha = 0.05$ were considered to have comparable Shannon-Wiener diversity indices between the two samplers. Similarly, mean species richness, abundance and volumes filtered were computed for the same 12 cruises. The relationship between sample volume and Shannon-Wiener diversity, abundance, or species richness, was explored to determine whether these metrics varied consistently with volume.

iii. Results

Data compared using either *t*-tests or Mann-Whitney U-tests showed that Shannon-Wiener diversity estimates (*h*) produced by ring nets and bongo nets were not significantly different for the ichthyoplankton assemblages present in Trinity and Conception Bays (Table 2-1, Figure 2-2). Coefficients of variation were 60% and 42% for bongo and ring nets respectively.

Species richness (SR) estimates showed statistically significant differences during the months of July 1985, August 1985 and August 1986 (Table 2-1, Figure 2-2). In July 1985 and August 1986 ring nets produced significantly higher estimates of richness. Bongo nets produced significantly higher estimates of richness in August 1985. Thus, in two of the three cases where significant differences were observed between the gears, ring net samples were found to estimate species richness of approximately 3.45 more species per tow than bongo nets (Table 2-1, Figure 2-2). In the one instance where bongo nets produced a higher estimate of species richness the difference was 0.78 (approximately one species) greater than for ring nets. In four out of six comparisons, the difference in species richness between the samplers was estimated to be less than one species and in instances where species richness differed by more than a single species, ring nets consistently produced higher estimates of richness. These results contradict the expectation based on sampling volume and conventional species-area theory. One sampler did not consistently sample more water than the other (Table 2-1). Bongo nets sampled more water most often, but ring nets produced higher estimates of richness. Analysis of Variance (ANOVA) showed significant difference between gears $F(1,682) = 133.725$; $p<0.001$, years $F(1,682) = 62.565$; $p<0.001$, and months $F(2, 682) = 144.534$; $p<0.001$ (Table 2-2).

Estimates of total abundance were statistically different between ring nets and bongo nets during the months of July 1985 and June 1986 (Table 2-1). In both of these instances, ring nets produced greater abundance estimates than bongo nets. No significant difference between gears was found in the remaining four comparisons. It

is possible that the differences were the result of the community being sampled and not as a result of differences in the efficiency of the gears. In instances where no significant differences were observed, the trends with regard to which sampler was estimating greater abundance was reversed relative to instances where differences were significant. Had the samplers been used to simultaneously collect samples it is possible that the differences observed in July 1985 and June 1986 would not have been apparent. Additionally, results such as those of Pepin and Shears (1997) predict that bongo nets, which generally filter a higher volume of water than ring nets, should produce a greater estimate of abundance. It is likely that the two comparisons showing significant difference did so as a result of differences in the community composition of larvae. Had these data been collected simultaneously it is believed that in the two comparisons showing significant difference, bongo nets would have produced greater abundance estimates than the ring net. An additional consideration, which was not addressed in the analysis but is discussed later in this chapter, is that the tow profiles for the samplers were different. Ring nets were towed at the surface and bongo nets were integrated over the water column.

The data showed that variances around mean values for Shannon-Wiener diversity and species richness were similar for both gear types. However, abundance estimates from ring nets appeared to be more variable than those from bongo nets (Figure 2-2). The catch ratios produced by dividing mean abundance estimates from bongo nets by mean abundance estimates from ring nets ranged from 0.160 – 1.68, demonstrating an order of magnitude difference between samplers in some instances but no consistent bias of

one sampler relative to the other.

Water volumes filtered by the two samplers showed significant differences during the months of June 1985, July 1985, June 1986 and July 1986. In all instances except June 1985, bongo nets filtered a greater volume of seawater than ring nets (Table 2-1, Figure 2-2). Contrary to expectation these data do not provide a clear pattern for interpretation. Surprisingly, no pattern between water volume filtered and species abundance, Shannon-Wiener diversity, or species richness was observed (Table 2-1, Figure 2-2).

iv. Discussion

Contrary to expectations, bongo and ring net comparisons carried out in this study did not identify any consistent bias in estimates of abundance, richness, or Shannon-Wiener diversity (Table 2-1); indeed most comparisons produced non-significant results and inconsistent trends among comparisons. The retrospective nature of this study meant that the potential variability introduced by different water masses contributed to variability of results but could not be separated from gear effects. Nonetheless, the fact that significant effects were rarely observed and were inconsistent in the patterns they showed suggests that any biases associated with sampling gear were minor compared to spatial and temporal variability among samples. Application of these findings in the context of commonly accepted ideas on

vertical distribution of larval fish, water mass variations, and sampling bias provided insight into whether any long-term temporal changes within the larval community could be extracted in light of the different gear types used. The results presented here demonstrate that a simple "correction factor" is not appropriate because there are no consistent between-gear biases and strong differences between sampling time periods cannot be attributed to gear alone.

The differences in tow profiles of the samplers do not invalidate the comparisons presented here. Species with similar vertical distributions should produce diversity measures that are comparable using different gear types, which raises the question of whether there is a reasonable expectation of similar distributions. Studies by de Young et al. (1994) and Pepin et al. (1995) showed that 95% of the ichthyoplankton in Newfoundland waters are present in the upper 40 m of the water column (Baumann et al., 2003). Studies on vertical distribution by Sclafani et al. (1993) and Neilson et al. (1986) suggest that larval fish are likely to be most densely aggregated surrounding the pycnocline or, in the case of larva with diminished body condition, above the pycnocline. Monthly to weekly CTD profile data collected at station 27 (a long-term sampling location considered to provide representative data for the Avalon Peninsula region (Baumann et al., 2003)), show that during the months of June, July and August the thermocline and pycnocline rarely, if ever, exceed 60 m and are typically shallower (Fisheries and Oceans Canada, 2008). Studies of larval distributions considered in tandem with the CTD data from station 27 led to the expectation that bongo nets should produce higher estimates of diversity than ring nets because bongo

nets were integrated throughout the water column and therefore would have passed through the depths where larva would be expected to be most highly concentrated and would integrate over a greater range of microhabitats (below, above and through the thermocline). This was not the observed pattern, suggesting that any gear biases in the data were far lesser in magnitude than biological differences associated with space or time.

Wind-driven water mass variation and environmental changes were not incorporated into the analysis of this data however their effects require comment. Tian et al. (2003) identify two types of physical/environmental variation that affect biological activities; short-term variations such as wind stress and, more importantly, long-term, large-scale variations such as changes in seawater temperature, ice cover, sea level, freshwater discharge, salinity, upper ocean current fields, vertical mixing, deep convection, upwelling activity, and thermohaline circulation.

Conception and Trinity Bay are both affected by the inshore branch of the Labrador Current, where effects are strongest in the spring as cold water is transported into the bays (Davidson and de Young, 1995). Both bays receive relatively low freshwater discharge, and the water-mass exchange with the NE Newfoundland Shelf is therefore the major factor controlling salinity variations (de Young and Sanderson, 1995). Data collected in Conception Bay and used in this study was restricted to the area surrounding Bell Island. This region of the bay is not greatly influenced by changes in water mass characteristics unlike the western side of Conception Bay where water

mass replacement is substantial (P. Pepin, pers. comm.). As with the western side of Conception Bay, Trinity Bay is also susceptible to wind forcing which in the summer, during the time when the samples from this study were collected, is characterized by south-westerly offshore winds (Yao, 1986). Leggett et al. (1984) published data collected during the months of June – August 1982 that indicated cyclonic atmospheric pressure systems generating onshore winds that were large enough to synchronously influence water mass exchange over a large area of Newfoundland's east coast (~700 km of coastline). Studies conducted by Pepin et al. (2003) and Baumann et al. (2003) indicate that there is considerable mixing associated with the physical dynamics of Conception and Trinity Bays. In Conception Bay variations in copepod nauplii were found to reflect changes in sea surface temperature from one survey to the next and that these nauplii were not associated with specific water masses. The presence of a clockwise circulation field and an area of retention or convergence located in the northwestern quadrant of the system were also confirmed (Pepin et al., 2003).

Ohman and Lavaniegos (2002) studied hyperiid amphipod communities and showed that for low numbers of individuals (<100 per sample) rarefaction curves for bongo and ring nets were almost impossible to differentiate (lower abundances reduced the probability of collecting rare species). Smaller mesh size increases the retention of smaller and typically more abundant larvae (Pepin and Shears, 1997; Richardson et al., 2004) and may, in turn, contribute to greater likelihood of capture in ring net samples. Larger, less abundant species are known to have greater net avoidance capabilities

than smaller individuals, and it is therefore expected that nets with a larger mouth size which filter a larger volume of water will retain more rare species (Brinton and Townsend, 1981; Pepin and Shears, 1997). Pepin and Shears (1997) found that bongo nets provided higher abundance estimates than Tucker trawls for larvae <5 mm in length because of extrusion through the larger mesh of the Tucker Trawl. The opposite was found to be true for larger (>10mm), less abundant larvae that are better able to avoid nets with smaller mouth openings (McGowan and Fraundorf, 1966; Brinton and Townsend, 1981; Pepin and Shears, 1997; Rebstock, 2002). A significant effect of species-specific morphological characters has also been reported (Pepin and Shears, 1997).

Studies by Pepin and Shears (1997) and Pepin et al. (2005) found that sampling variability of bongo nets was significantly greater than the variability of Tucker trawls and that variability of the Continuous Underway Fish Egg Sampler (CUFES) was significantly greater than the variability of bongo nets for ichthyoplankton. In both studies, samplers that filtered a larger volume of seawater produced abundance estimates with lower variability. The data from this study showed that in half of the comparisons, bongo nets sampled significantly more water than ring nets; however, bongo nets had a larger coefficient of variation. Given that the tow times and speeds for both gears were similar, it is possible that the bongo nets filtered larger volumes of seawater than ring nets because of reduced clogging due to the coarser mesh size, larger mouth size and as a result of the differences in aspect ratio between the nets. Despite expectations, in cases where the bongo nets filtered significantly greater

amounts of water this did not translate into consistently greater estimates of diversity, richness or abundance for that gear type. This leads to the conclusion that in July 1985 and in July 1986 the biological variation was of greater magnitude than the variation resulting from sampling bias.

In the present study no clear pattern in total abundance or species richness between gear types was found. Ohman and Lavaniegos (2002) reported an overall difference in abundance estimates between ring nets and bongo nets for only two species of amphipods of 42 species sampled. The authors noted that correcting for multiple testing would result in all of the comparisons being non-significant. Ohman and Lavaniegos (2002) also examined 17 holozooplanktonic species and suggested that higher abundance estimates produced by bongo nets were a result of higher catchability of rare or highly aggregated species by these samplers. These factors are also likely responsible for the lack of correlation between volumes of seawater filtered and total abundance for either gear type in the current study. Increased avoidance may also have contributed to the differences in abundance and diversity between samplers found in both this study and by Ohman and Lavaniegos (2002) as a result of the bridle positioned in front of the mouth of the ring nets (Brinton and Townsend, 1981; Rebstock, 2002).

Despite the lack of consistent pattern for planktonic communities with regard to abundance estimates by the two gear types considered here, Rebstock (2002) pointed out that unless a net effect produces a consistent, measurable discrepancy in a time

series, the sampler effect is minor relative to the natural variability in the community itself. Based on a review of more than 10 studies, Rebstock (2002) concluded that net effects that produce a catch ratio between bongo and ring nets of less than 1.3 are inconsequential and are very unlikely to be detected without a large sample size. Rebstock (2002) goes on to suggest that in the studies reviewed, a ratio of 2.0 or greater may possibly prevent detection of biological patterns, but for studies with data showing increases of two orders of magnitude or greater the effect of still larger net ratios would be relatively negligible. Based on these arguments, and the bongo net to ring net catch ratios calculated for the six comparisons in the present study (< or = 1.6), it is concluded that the abundance data from the different samplers in this study is sufficiently comparable for use in larger temporal studies.

v. Summary

Based on the comparisons of this study and documented patterns in sampling bias, larval distributions and water mass variations I conclude that for the purposes of the present study, that bongo and ring nets produce comparable estimates of Shannon-Wiener diversity, species richness, and abundance Correction factors varied considerably in space and time, suggesting no universal value could be applied and no consistent bias in sampler efficiency could be identified. The variability associated with different time periods was far greater than differences observed between samplers, and although analyses that combine the two types of samplers will add additional sources of error, the error is small and inconsistent and the greatest concern is that it will make other effects more difficult to detect.

vi. Literature Cited

Baumann, H., P. Pepin, F.J.M., Davidson, F. Mowbray, D. Schnack, and J.F. Dower (2003) Reconstruction of environmental histories to investigate patterns of larval radiated shanny (*Ulvaria subbifurcata*) growth and selective survival in a large bay of Newfoundland. ICES Journal of Marine Science 60: 243-258.

Brinton, E. and A.W. Townsend (1981) A comparison of euphausiid abundances from bongo and 1-m CalCOFI nets. CalCOFI Report 22:111-125.

Davidson, F.J.M., and B. de Young (1995) Modeling advection of cod eggs and larvae on the Newfoundland Shelf. Fisheries Oceanography 4: 33-51.

Davidson, F. J. M., Greatbatch, R. J. and de Young, B. (2001) Asymmetry in the response of a stratified coastal embayment to wind forcing. Journal of Geophysical Research 106: 7001-7015.

De Young, B., B., Anderson, J. T. Greatbatch, R.J. and P. Fardy (1994) Advection-diffusion modeling of capelin larvae in Conception Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Science 51: 1297-1307.

Doyle, M.J., M.S. Busby, J.T. Duffy-Anderson, S.J. Picquelle, and A.C. Matarese (2002) Aspects of the early life history of capelin (*Mallotus villosus)* in the northwestern Gulf of Alaska: A historical perspective based on larval collections October 1977-March 1979. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-132, 32 p.

Fisheries and Oceans Canada. (2008/11/17). AZMP Hydroacoustic data Station History. In Home Science Data and Products. Retrieved 2008/12/03, from http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/hydro/station/hist-eng.html?a=0.

Fortier, L. and W.C. Leggett (1983) Vertical migrations and transport of larval fish in a partially mixed estuary. Canadian Journal of Fisheries and Aquatic Sciences 40: 1543-1555.

Hartley, H.O. (1950) The maximum F-ratio as a short cut test for heterogeneity of variances. Biometrika 37: 308-312.

Hewitt, R. P. (1980) Distributional atlas of fish larvae in the California Current region: northern anchovy, *Engraulis mordax* Girard, 1966 through 1979. California

Cooperative Oceanic Fisheries Investigation Atlas 28: 1-101.

Hutcheson, K. (1970) A test for comparing diversities based on the Shannon formula. Theoretical Biology 29: 151-154.

Johnson, D.L. and W.W. Morse (1994) Net extrusion of larval fish: correction factors for 0.333 mm versus 0.505 mm mesh Bongo nets. NAFO Scientific Council Studies. 20: 85-92.

McGowan, J. A. and V.J. Fraundorf (1966) The relationship between size of net used and estimates of zooplankton diversity. Limnology and Oceanography. 11: 456-469.

Neilson, J.D., R.I. Perry, P. Valerio and K.G. Waiwood (1986) Condition of Atlantic cod *Gadus morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator avoidance. Marine Ecology Progress Series 32: 229-235.

Ohman, M.D. and P.E. Smith (1995) A comparison of zooplankton sampling methods in the CalCOFI time series. CalCOFI Report 36:153-158.

Ohman, M. D. and B.E. Lavaniegos (2002) Comparative zooplankton sampling efficiency of a ring net and bongo net with comments on pooling of subsamples. CalCOFI Report 43: 162-173.

Pepin, P., J. A. Helbig, R. Laprise, E. Colbourne, and T. H. Shears (1995) Variations in the contribution of transport to changes in planktonic animal abundance: a study of the flux of fish larvae in Conception Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 52: 1475-1486.

Pepin, P. and T.H. Shears (1997) Variability and capture efficiency of bongo and tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. Canadian Journal of Fisheries and Aquatic Sciences. 54: 765-773.

Pepin, P., P.V.R. Snelgrove and K. P. Carter (2005) Accuracy and precision of the continuous underway fish egg sampler (CUFES) and bongo nets: a comparison of three species of temperate fish. Fisheries Oceanography 14: 432-447.

Pepin, P., Dower, J.F., and Davidson, F.J.M. (2003) A spatially explicit study of prey-predator interactions in larval fish: assessing the influence of food and predator abundance on larval growth and survival. Fisheries Oceanography, 12:19-33.

Rebstock, G. A. (2002) An analysis of a zooplankton sampling-gear change in the CalCOFI long-term monitoring program, with implications for copepod population abundance trends. Progress in Oceanography. 53: 215-230.

Richardson, A. J., E. H. John, X Irigoien, R. P. Harris and G. C. Hays (2004) How well does the Continuous Plankton Recorder (CPR) sample zooplankton? A comparison with the Longhurst Hardy Plankton Recorder (LHPR) in the northeast Atlantic. Deep-Sea Research Part 1: 51: 1283-1294.

Sclafani, M., C.T. Taggart and K.R. Thompson (1993) Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. Journal of Plankton Research 15: 413-435.

Sell, D. W. and M.S. Evans (1982) A statistical analysis of subsampling and an evaluation of the Folsom plankton splitter. Hydrobiologia 94: 223-230.

Sokal, R.R. and F.J. Rohlf (2000) Biometry. 3rd ed. W.H. Freeman and Company, New York.

Somerton, D.A. and D.R. Kobayaski (1989) A method for correcting catches of fish larvae for the size selection of plankton nets. Fishery Bulletin United States 87: 447-455.

Suthers, I. M. and K.T. Frank (1989) Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in Southwestern Nova Scotia determined with two different gear types. Canadian Journal of Fisheries and Aquatic Sciences. 46: 591-602.

Taggart, C.T. and W.C. Leggett (1984) Efficiency of large-volume plankton pumps, and evaluation of a design suitable for deployment from small boats. Canadian Journal of Fisheries and Aquatic Sciences 41: 1428-1435.

Tian, R.C., D. Deibel, R.J. Thompson and R.B. Rivkin (2003) Modeling of climate forcing on a cold-ocean ecosystem, Conception Bay, Newfoundland. Marine Ecology Progress Series 262: 1-17.

VanGuelpen, L., D.F. Markle and D.J. Duggan (1982) An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. Conseil International Pour l'Exploration de la Mer. 40:226-236.

Yao, T. (1986) The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmosphere-Ocean 24: 235-252.

Figure 2-1: Sampling sites where data were collected in Trinity and Conception Bays during the summers (June-Aug) of 1985 and 1986. Samples from Trinity Bay were collected using Bongo nets and samples from Conception Bay were collected using Ring nets.

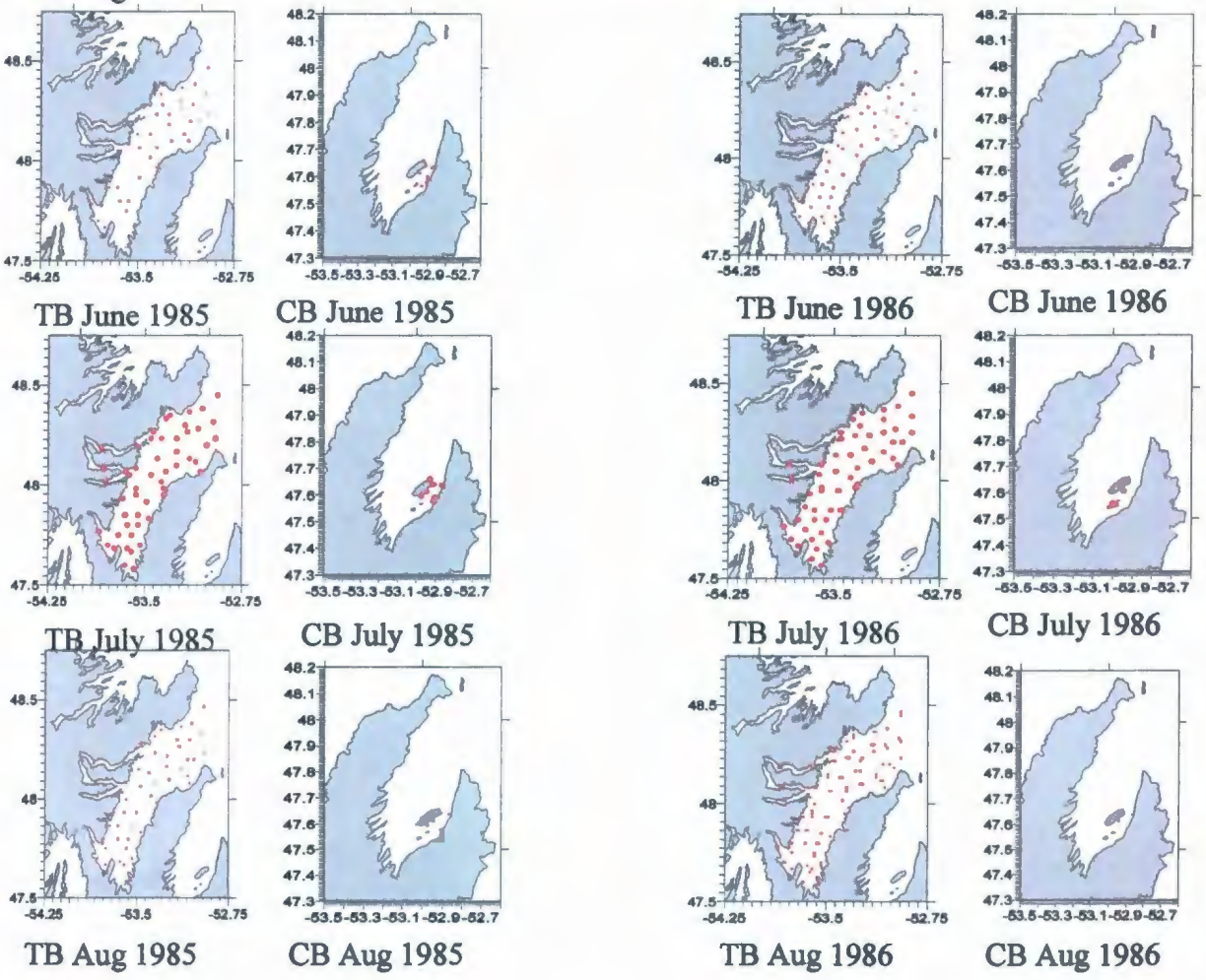

Figure 2-2: a. Mean Shannon Diversity, b. Species Richness, c. Species Abundance (/1000m3) and d. water volume filtered from samples collected using Bongo Nets or Ring Nets. Error bars represent standard deviation, circles and triangles represent the mean values for each cruise.

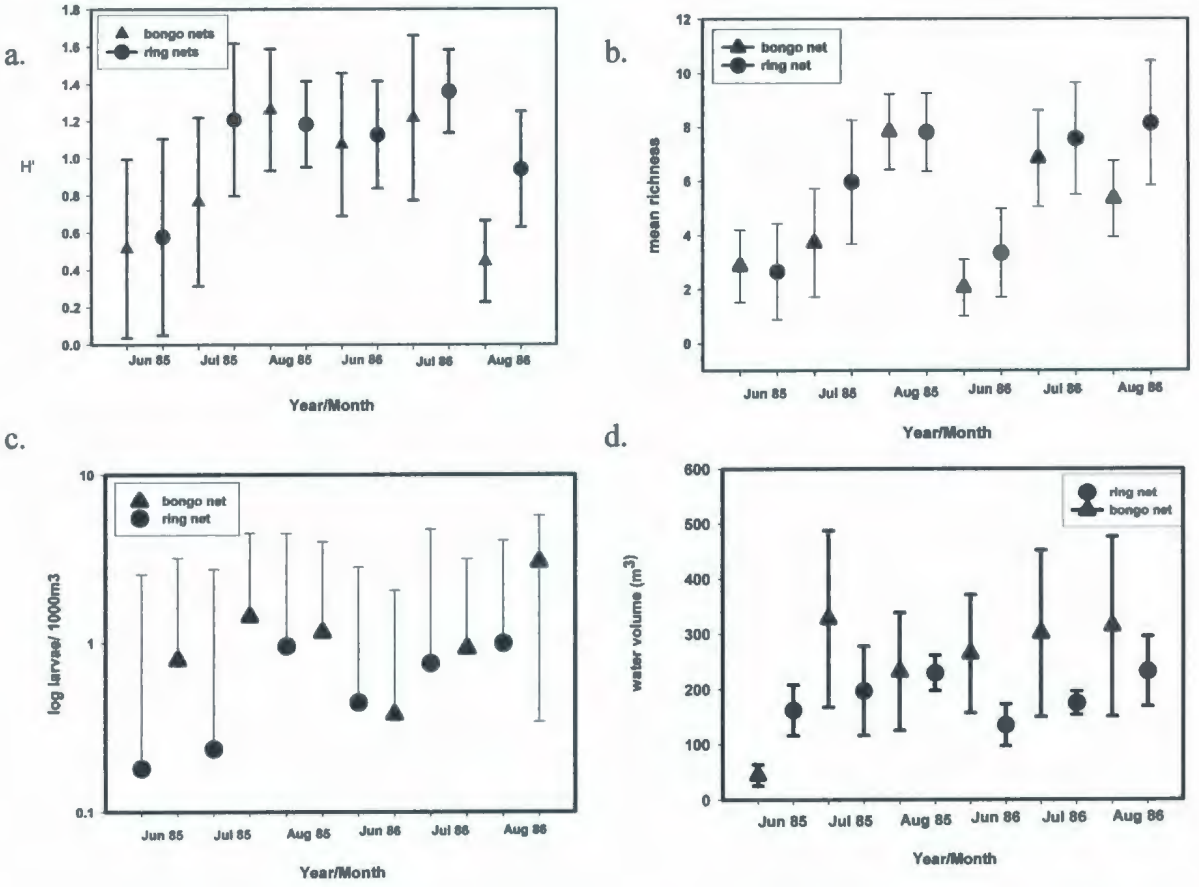

Table 2-1: Mean species richness (SR), Shannon diversity (H'), abundance (/1000m^3) and water volume filtered shown for bongo and ring net cruises used in gear comparisons. Mean values were calculated using non-transformed data.

Bay	Gear	Date	H'	p	SR	p	Abundance	p	Water Volume	p
Conception Bay	Ring Net	June 3-27 1985	0.58	>0.9	2.72	0.223	130.36	0.712	161.9	0.000
Trinity Bay	Bongo Net	June 19-24 1985	0.52		2.16		147.14		44.43	
Conception Bay	Ring Net	July 12-31 1985	1.20	>0.4	7.20	0.000	1066.53	0.000	196.93	0.000
Trinity Bay	Bongo Net	July 18-24 1985	0.77		4.04		169.41		327.4	
Conception Bay	Ring Net	Aug 1-27 1985	1.18	>0.5	7.89	0.013	1511.01	0.067	229.52	0.621
Trinity Bay	Bongo Net	Aug 16-21 1985	1.26		8.67		1950.00		231.89	
Conception Bay	Ring Net	June 18-26 1986	1.13	>0.5	4.8	0.484	451.12	0.000	135	0.000
Trinity Bay	Bongo Net	June 18-23 1986	1.07		5.05		158.36		264.07	
Conception Bay	Ring Net	July 9-23 1986	1.36	0.436	8.85	0.395	1250.34	0.066	174.75	0.001
Trinity Bay	Bongo Net	July 18-24 1986	1.22		8.42		2098.15		300.78	
Conception Bay	Ring Net	Aug 7-14 1986	0.94	>0.1	9.21	0.000	1021.49	0.489	232.19	0.108
Trinity Bay	Bongo Net	Aug 20-26 1986	0.44		5.47		1267.52		313.39	

Table 2-2: Analysis of Variance (ANOVA). Species richness from data collected during June-Aug 1985 and 1986 was used as the dependent variable with month, gear type and year used as factors.

Dependent Variable: richness

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	2891.439[a]	11	262.858	76.461	.000
Intercept	18101.884	1	18101.884	5265.520	.000
gear	459.722	1	459.722	133.725	.000
year	215.088	1	215.088	62.565	.000
month	993.761	2	496.881	144.534	.000
gear * year	51.726	1	51.726	15.046	.000
gear * month	1.474	2	.737	.214	.807
year * month	456.111	2	228.055	66.337	.000
gear * year * month	295.017	2	147.508	42.908	.000
Error	2344.590	682	3.438		
Total	28360.000	694			
Corrected Total	5236.029	693			

a. R Squared = .552 (Adjusted R Squared = .545)

III. Temporal Variation In Community Composition Of Fish Larvae In Coastal Newfoundland

i. Introduction

Multiple hypotheses have been invoked to explain the dramatic declines that took place in the early 1990's in Northwest Atlantic demersal fish stocks (Helbig et al., 1992; Taggart et al., 1994; Gomes et al., 1995; Hutchings, 1996; Colbourne et al., 1997; Gerasimova and Kiseleva, 1998; Parsons and Lear, 2001; Lilly and Carscadden, 2002; Rose, 2003; Drinkwater and Gilbert, 2004; Colbourne, 2004; Carscadden, 2005; Frank et al., 2005). Although the major collapse of the groundfish stocks occurred at the beginning of the 1990's, and moratoria or severe limits have been imposed on cod fishing in most areas since 1992, many stocks have failed to recover over the past decade. Major changes in community composition and abundances of adult fishes on the eastern Newfoundland coast have been attributed to the commercial exploitation of a once prosperous natural resource (Gomes et al., 1995; Hutchings, 1996; Rose et al. 2000, 2003). However, there has been discussion as to whether extreme environmental conditions associated with cold water (Gomes et al., 1995; Hutchings, 1996) exacerbated the widely accepted impact of overfishing (Taggart et al., 1994) during this shift in species composition. Gomes et al. (1995) assessed community shifts in adult fish stocks before and during the time of the fisheries collapse; however, a parallel assessment of potential shifts in larval fish communities has not previously been completed. Larval fish communities can provide additional insights into community shifts because larval surveys typically include a wider array of species than those targeted by, or removed as bycatch from, commercial or research vessel sampling. Sampling of early life stages targets a wider variety of life history strategies

and habitat uses than is available from traditional research vessel surveys that often exclude coastal areas, and may therefore provide a significant contribution to the literature related to climate and fisheries.

Gomes et al. (1995) reported a decline in adults of six non-commercial fish species prior to the major declines in more abundant species such as cod during the early 1990's. These declines occurred in broadhead wolfish, thorny skate, roughhead grenadier and witch flounder in 1985, and Greenland halibut in 1988. Taggart *et al.* (1994) provided a comprehensive assessment of the Atlantic cod (*Gadus morhua)* fishery and biology in the Newfoundland region from 1880 through the early 1990s. Specifically they described increases in fishing pressure during the 1960's when foreign fleets extended their ranges. Fish landings are reported to have increased from approximately 300,000 t in 1960 to over 800,000 t by 1968 (Rose et al., 2000). These increases represented an order of magnitude change in fishing effort relative to the long-term average (150-300,000 t/year) based on 400 years of fisheries in the region (Rose, 2003; Harris, 1990 in Rose, 2004). The increased effort was quickly followed by steep declines in catch during the 1970's ($< 2 \times 10^5$ t), and the subsequent introduction of total allowable catch limits (TAC) in 1974 in addition to the establishment of the Canadian 200 mile exclusive economic zone (EEZ) in 1977. Fishing pressure targeting Atlantic cod increased again during the mid 1980's prior to dropping off to $< 1 \times 10^5$ t during the early stages of the fisheries closure in 1991-92 (Taggart et al. 1994; Dept. of Fisheries and Oceans, 2005). Effectively all Canadian Atlantic cod stocks (2J3KL, 3NO, 3Pn-4RS, 4T, and 4VsW) declined in the early to

mid-1980's under extreme fishing pressure (deYoung et al., 1999). Throughout the 1960's, during peak fishing pressure in Newfoundland, haddock (*Melanogrammus aeglefinus*) populations also experienced steep declines that resulted in commercial extinction (Rose, 2003). This same scenario is also true for redfish species (*Sebastes* spp.) in eastern Newfoundland and in the northern ranges off Labrador (Rose, 2003). Declines in redfish are believed to be a result of a targeted fishery by Russian trawlers during the 1960's (Rose, 2003). Capelin (*Mallotus villosus)* was traditionally unimportant as a commercial fishery in Newfoundland (<20,000 t/year), however, Russian fishery vessels removed > 350,000 t/year during the 1970's (Rose, 2003). By the late 1980's capelin were exhibiting slow growth, delayed spawning, and an expansion in their historical distribution (Frank et al., 1996). Thus, although the magnitude and timing of declines varied within different Newfoundland regions and among taxa, it is generally accepted by many authors that the significant changes that occurred in the fishes of Newfoundland waters since the 1980s were predominantly the result of overfishing.

In addition to fishery-induced changes, numerous authors have linked fish diversity, abundance, distribution, condition, and prey availability to oceanographic conditions such as temperature and salinity (Gomes, 1995; Frank et al., 1996; Rose, 2003; Worm et al, 2005). Rose (2003) summarizes many of the shifts that occurred in species distributions, abundance and prey items during the early 1990's. These changes were observed not only in fish species, but also in organisms as different as larvaceans (*Oikopleura sp.*) and sea birds such as gannets (Rose, 2003). Some of these changes,

such as those in *Oikopleura* sp., are often the result of wind-driven water mass exchanges in Newfoundland embayments (Taggart and Frank, 1987).

Newfoundland waters are characterized by short-term (day scale) and strong seasonal variations as a result of variation in atmospheric forcing (i.e.: air temperature and wind stress) and, during some times of year, extent of sea ice (Petrie et al., 1991; Colbourne, 2004). More detailed discussion of short term water mass affects on the current study's data is presented in Chapter 2. Inshore embayments are physically dynamic, and are closely related to the adjacent shelf system (deYoung and Sanderson, 1995). Upwelling and downwelling patterns within Trinity and Conception Bay, two large embayments on the North coast of the island, are driven primarily by offshore and onshore wind patterns. These events create substantial water mass variations.

Substantial large-scale inter-annual variations in temperature and salinity have been recorded in the northwest Atlantic Ocean on multiple occasions throughout the last century (Dickson et al., 1988). These patterns are significantly correlated with the North Atlantic Oscillation (NAO) index, which is measured as "the difference in sea level atmospheric pressures between the Azores and Iceland and is a measure of the strength of the winter westerly winds over the northern North Atlantic" (after Rogers, 1984 in Drinkwater et al., 2001). These anomalous temperature variations loosely correlate with increases or decreases in biomass of biological communities (Dickson et al, 1988; Taggart et al., 1994; Rose, 2003) and the NAO has been shown to correlate strongly with biological production (Tian et al., 2003). Dickson et al. (1988) describe

in detail the progression of the "Great Salinity Anomaly" of the North Atlantic during 1968-1982, where cold, less saline water reached Newfoundland during 1971-72. Taggart et al. (1994) report an order of magnitude decline in fisheries landings and in biomass estimates for Atlantic cod during that same time frame. Taggart et al. (1994) also report reduced cod recruitment during the anomalously cold temperature period that began in 1983 and continued through the early 1990's with only brief warming during 1986 and 1987 (Colbourne et al., 1994 in Taggart et al., 1994; Drinkwater, 1996; Colbourne et al., 1997; Rose, 2003; Drinkwater, 2004; Colbourne, 2004). Colbourne (2004) points out that not only did the 1990's represent the third consecutive decade with below-average water temperatures, but the negative salinity anomaly on the inner Newfoundland Shelf during the 1990's was analogous to that experienced during the "Great Salinity Anomaly" of the early 1970's. Clearly, climate may play a significant role in population dynamics of marine fishes.

Fisheries-induced changes in community composition of larval fishes might be expected to differ from those related to annual weather variation. Species such as cunner, blennies, and snailfish that have not been targeted by fisheries and utilize nearshore environments that should presumably make them less vulnerable as bycatch should be unaffected by overfishing. If, however, environment has played a role, then they may exhibit similar patterns of variation as other (targeted) species. Different spawning strategies might also produce different scenarios. For example, Snelgrove et al. (2008) suggested that pelagic larvae of bottom spawners may be less vulnerable to advective loss associated with temperature-dependent egg development than larvae

that hatch from pelagically-spawned eggs; it might be expected that if cold temperature was a factor driving the ground fish collapse, then species with demersal eggs might be less vulnerable to cold periods and better able to recover after cold periods. Pelagic eggs would be more likely to be advected and die offshore before they have had a chance to hatch and swim to a "safe site" (Frank and Leggett, 1983), meaning that larvae of demersal spawners should occur in greater proportions in years with cold summer temperatures.

The goal of the current study is to examine historical ichthyoplankton datasets in order to determine how these assemblages have changed during this period of significant change in groundfish. Because these assemblages encompass a greater variety of species than commercial fisheries and include species that are of limited vulnerability to these fisheries, they offer potential insights into the relative roles that overfishing and environmental variation have played in the changes that have occurred in fish communities in Newfoundland waters.

ii. Methods

Data Collection

Data used in this study were collected during the summers (May-September) of 1982 – 2002 from three Newfoundland embayments; Trinity Bay, Conception Bay and Placentia Bay (Figure 3-1). Trinity Bay is located on the northeast coast of Newfoundland and measures approximately 100 km long by 30 km wide, with a maximum depth of 630 m near the bay's centre. A sill that traverses the mouth of the

bay has a maximum depth of 240 m. Wind forcing has a major effect on the stratification and circulation of the Bay (Yao, 1986; Davidson et. al., 2001). During the summer months, southwesterly offshore winds are prominent and create areas of upwelling (deYoung and Sanderson, 1995). Conception Bay is approximately 50 km long by 25 km wide with a maximum depth of roughly 300m and a sill at the mouth of the bay at 150 m depth. Like Trinity Bay, Conception Bay is susceptible to local wind forcing (Pepin et al., 1995). Placentia Bay is located on the southeast coast of the Avalon Peninsula and runs along a longitudinal axis that is ~25° east of north (Bradbury et al., 2000). Placentia Bay measures approximately 130 km long by 100 km at its widest point near the mouth of the bay and depths up to several hundreds of meters; predominant currents flow into the bay along the eastern shore and out along the western shore (Bradbury et al., 2000).

Data from Trinity Bay were collected using either a 61 cm Bongo net (side unspecified) fitted with 333 or 505 μm Nitex mesh, or a 2 m x 2 m (mouth opening) Tucker trawl fitted with 1000-, 505-, and 333- μm mesh sections. Data from Conception Bay was collected using either a 50- cm ring net fitted with 165 μm mesh or the 4 m^2 Tucker trawl. Each Bongo net or Tucker trawl sample consisted of an oblique tow of approximately 15 min at a tow speed of approximately 2-3 kn. The bongo nets and Tucker trawls were lowered to a depth approximately 5-10 m from the sea floor in shallow areas or most often to a maximum depth of 50 m. During several surveys in the early 1980's nets were lowed to a maximum depth of 200 m. Each ring net sample consisted of a single horizontal tow of approximately 15 min at a tow

speed of roughly 2-3 kn at a fixed depth of 7m. Surveys in both Trinity and Conception Bays differed in design and coverage among years and gear types (Chapter 1). Data from Placentia Bay were collected along a grid of 45 stations (Figure 3-2) that were sampled using the 4 m^2 Tucker trawl as described above, except that tows were to 40m depth (Bradbury et al., 2003). For all tows, volume filtered was estimated using a General Oceanics flowmeter positioned at the mouth of each net. Refer to Table 1-1 for a summary of gear type usage by bay and year.

Data Analysis

The seasonal data: Placentia Bay

A null model of expected seasonal variability was generated from the data collected in 1997, 1998, and 1999 in Placentia Bay. These data were collected consistently using the same gear, at the same sites, at similar periods each year, and for multiple years. Therefore, differences in community composition were interpreted to be as a result of differences in season and spatial location, and not a result of gear differences or other differences in data collection. These data were examined for trends that could thus be attributed to time (i.e. seasonal patterns in community composition) and space (i.e. differences in community composition at head of the bay versus the mouth of the bay as described in Chapter 4), and provided a basis on which to examine the remainder of the available data sets.

Creation of the null model was achieved by first generating a species by sample matrix using standardized values (larvae·1000m^{-3}) from the 1997, 1998 and 1999 Placentia

Bay data. Data were then fourth-root transformed (Field et al., 1982) and a station-by-station matrix of Bray-Curtis similarity was generated within the software package Primer-Express Version 5.2.9. (Plymouth Routines In Multivariate Ecological Research). The multivariate analyses described below were all completed in PRIMER-E except where stated otherwise. A common characteristic of marine survey data is that many of the species are absent from a large number of the samples. Typically greater than half the data matrix entries are zeros and transformation of the data does not change this (Field et al., 1982) Bray-Curtis is a widely used similarity measure that is unaffected by joint absences (zero values) in between-sample comparisons (Clarke, 1993). There are instances species depauperate data sets such as those seen in many pollution and colonization studies where joint absences can be meaningful and should be addressed by using a zero-adjusted Bray-Curtis coefficient (Clarke et al., 2006). However, the effect of a zero-adjustment to Bray-Curtis in the data presented here, in which there are no exceptionally impoverished samples should be negligible (Clarke et al., 2006). The similarity matrices were then used to generate group average cluster and multi-dimensional scaling (MDS) plots to determine whether samples collected at similar times within or among years were more similar in species composition than those separated in time. Based on the levels of similarity observed among seasons and years in this analysis, an expectation was formulated of which species dominate communities and what species are relatively rare at various times of the year. Given the possibility of major physical changes in very short time periods (days to weeks), and the difficulty of interpreting this change I felt it was critical in this study to look for consistency in response over different spatial and temporal scales.

Similarity percentages (SIMPER) (Clarke, 1993) were used to determine which species were primarily responsible for Bray–Curtis dissimilarities among months and years given that the presence of seasonal variation in community composition of larvae has been established by other authors (e.g. Methvan et al.,2001). SIMPER analysis estimates the contribution of individual taxa to similarity among treatments and is used to determine the extent to which individual species were responsible for patterns detected by MDS. Groupings used for comparison, to identify percentage contributions by individual taxa to overall dissimilarity among assemblages, were created using factor designations based on group average cluster results or by grouping the data by year of sampling (e.g., Caldeira, 2002).

To identify seasonal trends, species abundance was plotted by day of year in exploratory analysis for each species for all years of the data set. Plots based on Placentia Bay null model were used to generate an expectation as to how communities vary seasonally. Specifically, species richness and concentrations of the five most abundant species in each seasonal grouping were identified. This expectation made it possible to determine whether community composition from other surveys and other years, collected during individual unrelated surveys, were consistent with the seasonal expectation or whether they differed markedly. Species compositions that differed considerably (produced discrete groupings based on cluster analysis (Sneath and Sokal, 1973) and MDS) from the seasonal norm were then attributed to variations in space or environment above and beyond season.

The long-term data: Conception and Trinity Bays

The analysis described above was then repeated separately for all data collected in Conception Bay and for all data collected in Trinity Bay. These data span a much broader time period relative to the Placentia Bay null model. Conception Bay and Trinity Bay data encompass the years, 1985-1998 and 1982-2002 respectively, but incorporate different gear types, as discussed in detail in Chapter 2. The Placentia Bay analyses clearly indicated a strong seasonal signal, so each summer month was analyzed separately for a given bay, incorporating all available ichthyoplankton data irrespective of gear type. The data available for specific months in a given year varied among bays, necessitating separate analyses by bay as well as month.

An additional approach that was added for the long-term data comparisons was the use of ANOSIM, a PRIMER-E routine that is analogous to ANOVA that allows statistical evaluation of differences among sample groups identified a priori. In this case, ANOSIM was used to test whether some of the general long-term temporal patterns identified in the MDS and cluster analyses were statistically different. The dendograms produced using cluster analyses are not presented here because the large numbers of samples meant that these figures were exceedingly cumbersome and impossible to present in a readable thesis format. Nonetheless, patterns were very consistent with the MDS plots that are shown.

The final evaluation involved the computation of mean Shannon-Wiener diversity (H)

and species richness (*SR*) for each individual month, which was then compared by month across multiple years using analysis of variance (ANOVA). Species richness (SR) was defined as the number of different species present in a sample collected at a single station and was obtained by using the diversity function in the program Primer-E. These data were then used to identify trends in diversity *(H)* and species richness *(SR)* through time. A variation on this theme was to compare diversity and species richness among temporal groupings identified by the cluster analyses described above. Thus, each sample was assigned to a time period grouping based on the clustering analysis Shannon-Wiener diversity was computed using the formula:

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where H is the diversity in s species, s is the number of species present in the sample, p_i is the proportion of species i in the sample (n_i/n), and $\sum p_i = 1$. An estimate of H is therefore,

$$H = -\sum_{i=1}^{s} (n_i / n) \ln(n_i / n) \qquad (2)$$

given a random sample of n (total number of individuals in the sample from all species) observations from data in the s species i (1, 2, . . ., s) with probabilities p_i (1, 2, . . ., s), where h and H fall between zero and ln s (Hutcheson, 1970).

iii. Results

Seasonal Variation – Placentia Bay Null Model (1997-1999)

Multi-dimensional scaling plots created using Placentia Bay data identified a seasonal pattern characterized by the occurrence of two distinct larval fish communities, one in the spring (April/May) and the other in late summer (August/ September) (Figure 3-3). The two clusters of stations that resulted from the analysis are also represented in the MDS plot (Figure 3-3a) and are comprised of stations sampled during all three years; stations from each year did not fall into their own separate clusters. It was therefore necessary to determine what caused these stations to be more similar to stations sampled during different years than to stations sampled within the same year. Figure 3-3b is a representation of the same ordination with the station symbols coloured to highlight the month when the stations were sampled. This plot shows three tight clusters and a gap between the June stations and the August/September stations where the unsampled July period might potentially have fallen. This monthly pattern within the larval fish community likely represents strong seasonal variation. The three groups that are shown in figure 3-3b were then examined to identify which taxa were responsible for the different clusters.

The spring (April) community consisted of 29 taxa, where the five most abundant taxa were: sandlance (*Ammodytes* sp.), Arctic shanny (*Stichaeus punctatus)*, shorthorn sculpin (*Myoxocephalus scorpius*), radiated shanny (*Ulvaria subbifurcata)* and snailfish (*Liparis* sp.). Several other flatfish and sculpin species were also among the most abundant species captured during the spring. The late summer (August)

community consisted of 20 species, where the five most abundant species were: capelin *(Mallotus villosus),* cunner (*Tautogolabrus adspersus),* fourbeard rockling (*Enchelyopus cimbrius),* red fish (*Sebastes* sp.) and Atlantic cod (*Gadus morhua).* Radiated shanny (*U. subbifurcata*) were also among the most abundant species captured during late summer. A less diverse seasonal "transition" community was present during the month of June and was comprised of 13 species; no data was available for the month of July (Table 3-1).

SIMPER analysis on seasonal classifications defined using group average cluster analysis identified capelin *(M. villosus,* 22.18%), cunner (*T. adspersus,* 19.09%), sandlance (*Ammodytes* sp., 14.58%), fourbeard rockling (*E. cimbrius,* 4.46%) and Atlantic cod (*G. morhua,* 4.15%) as the top five species responsible for differences between the spring and late summer assemblages. These five species together were responsible for 64.46% of the dissimilarity between the two communities. These differences represent the presence of capelin, cunner and fourbeard rockling in August. These species were absent from stations sampled in April and May. Additionally, sandlance were present at the spring stations and were absent from the summer stations. Atlantic cod were present in samples from both spring and summer but the average abundance was higher (~1 ind/1000m^3 vs. ~3 ind/1000m^3) at stations sampled in August. SIMPER analysis carried out on yearly groupings (ignoring months) revealed that between years there was an average dissimilarity of 78.34%. Between stations within a single year there was an average similarity of only 24.80%. sandlance (*Ammodytes* sp.) was the discriminating species that was consistently

responsible for differences among years and was also among the largest contributors to dissimilarity (1997 and 1998 = 13.02%; 1997 and 1999 = 14.10%; 1998 and 1999 = 10.76%). Sandlance (*Ammodytes* sp.) was also the largest contributor to dissimilarity within years (1997 = 60.55%; 1998 = 26.96%; 1999 = 40.78%). Other species that consistently contributed to dissimilarity both between and within years were capelin (*M. villosus)* and cunner (*T. adspersus).* All three of these species were present in relatively high abundances throughout the sampling period. Therefore, it is likely that these species were responsible for much of the among-year dissimilarity given that their average abundance varied greatly from year to year (e.g. capelin - 1997 ~ 194/1000m^3 vs. 1998 ~240/1000m^3).

Multi-dimensional scaling and group average cluster plots created using Conception Bay data (1985-1998), confirmed the presence of a seasonal pattern similar to the pattern identified in Placentia Bay. Further break down by month (June, July and August) revealed inter-annual patterns of variation in the data, which is examined below. Similar seasonal/monthly patterns were also found for Trinity Bay.

Consistency in the seasonal pattern across bays (Placentia, Trinity and Conception Bays) motivated the break down of data by month to assess better the patterns of interannual variation.

Inter-Annual Data Comparisons: Conception and Trinity Bays

Conception Bay – June (1985-1986, 1990)

Multi-dimensional scaling plots and group average cluster analysis of Conception Bay June data (1985, 1986 and 1990) resulted in the classification of three main temporal groups; a mixture of stations from 1985/86, 1986 only, and 1990 (Figure 3-4). The 1985/86 mixed grouping showed some within-group separation between years and SIMPER analysis indicated that this group had only 33.07% similarity among stations. The 1986 only and the 1990 groupings showed 71.29% and 70.11% similarity, respectively. Between-group differences were most prevalent for the comparisons of the 1985/86 mixed group and the 1986 only group, which indicated a dissimilarity of 71.79%. The top five discriminating species in this comparison were winter flounder (*Pseudopleuronectes americanus,* 20.40%), snailfish, (*Liparis* sp., 17.25%), radiated shanny (*U. subbifurcata,* 17.24%), American plaice (*Hippoglossoides platessoides,* 14.56%) and. Atlantic cod (*G. morhua,* 11.26%). Combined, these species were responsible for 80.70% of the dissimilarity between these groups. The 1986 only group had a much higher average abundance of winter flounder (~149 ind/1000m^3) than did either the 1985/1986 mixed group (~3 ind/1000m^3) or the 1990 group (~1 ind/1000m^3). The same was true for each of the other four species that were the primary contributors to the differences between the 1985/86 mixed group and 1986 group. These high concentrations were not present in all of the June 1986 stations and are therefore related more to spatial patchiness of ichthyoplankton abundance rather than a consistent temporal pattern. Figure 3-5 also supports this conclusion as it shows that these five species showed co-occurrence of more than 50%. The discrete cluster of stations from 1990 is visible in the inset of figure 3-4, and shows that, despite an overlap in similarity of stations in 1985 and 1986, there is no overlap with stations

from 1990.

The analysis of similarity (ANOSIM) showed significant difference between groups (Global $R = 0.163$; $p = 0.001$). All three groups showed significant difference with the 1985/86 mixed group and the 1986 only group having values of R = 0.201; p = 0.001, the 1990 and 1986 only groups showed values of R = 0.858; p = 0.001 while the 1985/86 mixed group and the 1990 group had values of R = 0.122; $p < 0.02$. The 1985/86 mixed group and 1990 group comparison were 67.70% dissimilar. The major discriminating species in this comparison were American plaice (*H. platessoides,* 17.77%), radiated shanny (*U. subbifurcata,* 13.76%), Atlantic cod (*G. morhua,* 12.40%), redfish (*Sebastes* spp., 10.76), and Atlantic sea snail (*Liparis atlanticus)* (7.40%). These species combined accounted for 62.09% of the dissimilarity between groups. These species showed similar co-occurrence of approximately 30% (Figure 3-5). Because of the discrete clustering of stations in 1990, the differences between the groups were considered to be a result of changes in community composition among time periods and not the result of spatial differences within the bay.

Shannon-Wiener diversity and richness values from the groupings before 1990, and the year 1990 were compared using ANOVA to determine whether the groups were significantly different communities in terms of diversity measures. ANOVA revealed that these groupings did not have significantly different diversities $F(1,126) = 0.251$; $p>0.05$ however did show significantly different richness $F(1,126) = 182.124$; $p<0.001$. Interestingly although overall diversity from the mid 1980's was not

significantly different from that in 1990 species richness in June of 1990 was significantly higher than during the mid 1980's.

Co-occurrence of Taxa

Multi-dimensional scaling plots and group average cluster analysis identified groups of several species that co-occur (Figure 3-5). Species with the greatest similarity of occurrence (60-65%) were shorthorn sculpin (*Myoxocephalus scorpius*) and inquiline snailfish (*Liparis inquilinus*). Atlantic cod (*G. morhua*) and American plaice (*H. platessoides)* also showed 60-65% similarity of occurrence. In instances where individuals could not be identified beyond family level, typically because of damage during capture, members from the Cotidae and Stichaeidae families showed 100% co-occurrence.

Conception Bay - July (1985-1986, 1990-1994, 1997-1998)

Multi-dimensional scaling plots and group average cluster analysis of Conception Bay July data (1985, 1986, 1990-94, 1997 and 1998) (Figure 3-6a) identified three clusters of yearly groups that showed similar community composition. A cluster formed from data collected in 1985 and 1986, another for 1990 to 1993 and another group for the years 1994, 1997 and 1998 (Figure 3-6b). Stations from 1985-86 and 1994, 1997-98 were more closely clustered to one another than they were to stations sampled in 1990-1993. This pattern is contrary to the expectation that stations sampled more closely in time would be more similar in species composition. The analysis of

similarity (ANOSIM) showed significant difference between groups (Global $R = 0.297$; $p = 0.001$). All three comparisons (1985-86/1990-93, 1985-86/1994-98 and 1990-93/1994-98) showed difference at a significance level of 0.1%. SIMPER analysis that compared data groups collected pre- and post-1992 identified capelin (*M. villosus,* 14.48%), American plaice (*H. platessoides,* 11.13%), winter flounder (*Pseudopleuronectes americanus,* 8.86%) yellowtail flounder (*Limanda ferruginea,* 8.72%), and Atlantic cod (*G. morhua,* 8.54%) as the discriminating species, with a total dissimilarity of 51.73%. These species, in combination with an additional seven species combined to account for 90.52% of the dissimilarity between the pre and post 1992 groups. In all cases the average abundance for each of the above listed species was lower post 1992 than it had been in the years before 1992.

Community composition in 1991 and 1992 differed from previous years. July 1991 was the only year when capelin (*M. villosus)* larvae were not present during that month, whereas cunner (*T. adspersus),* yellowtail flounder (*Limanda ferruginea)* and witch flounder (*Glyptocephalus cynoglossus*) larvae were completely absent in both 1991 and 1992. Capelin (*M. villosus)* larvae, although present in 1992, were in very low abundances relative to preceding years. Atlantic cod (*G. morhua*) larval abundances were lower in 1991 and 1992 compared with previous years, but increased thereafter. Arctic cod (*Boreogadus saida*), redfish (*Sebastes* spp.), varigated snailfish (*L.s gibbus)*, Arctic shanny (*S. punctatus)*, blennies (*Lumpenus* sp.), and Atlantic poacher (*A. decagonus)* were also present in higher abundances during 1991 than in other years (Figure 3-7). Prior to 1991, Arctic shanny abundances generally peaked

during the months of May and June.

Shannon-Wiener diversity and richness values from the groupings before 1990, 1990-1993, and after 1993 were compared using ANOVA to determine whether the clusters represented significantly different communities in terms of diversity measures. ANOVA revealed that the groupings showed significantly different diversities $F(2,519) = 39.946$; $p<0.001$ and richness $F(2,519) = 34.017$; $p<0.001$. Thus, the ichthyoplankton present in Conception bay during the month of July changed significantly from the mid 1980's to the late 1990's; exhibiting a less diverse and less species rich community.

Conception Bay - August (1985-86, 1994, 1997-98)

Multi-dimensional scaling and group-average cluster plots created using August data from Conception Bay also revealed the presence of a dissimilarity in community composition during the early 1990's (Figure 3-8). The pattern was more clearly demonstrated by the August data than July data because data were unavailable for the anomalous years of 1991 and 1992. As can be seen in figure 3-8 the years 1985-86 were clustered more closely with stations from within those years than with stations from 1994 or 1997-98. A similar cluster separated in the 3rd dimension represents stations from 1994. Again 1994 stations clustered more closely with stations sampled within that year than with stations sampled during other years. Therefore, stations sampled in 1985-86 were more similar in species composition to one another than they were to stations from 1994 or from 1997-98. This is also true for the two additional

clusters comprised of stations from 1994 and the last cluster comprised of stations from 1997-98. The stations contained in each of the clusters suggests that stations sampled more closely in time were generally more similar in species composition than stations separated in time. However, the clusters in figure 3-8 showing the 1994 stations separated from the other two clusters along the 3rd dimension, further suggesting that the community composition of the stations sampled were no more similar to those sampled more closely in time and that there are distinct clusters present from before and after the early 1990's period.

The analysis of similarity (ANOSIM) showed significant difference between groups (Global $R = 0.621$; $p = 0.001$). All of the comparisons between groups showed difference at a significance level of 0.1%. SIMPER analysis identified witch flounder (*G. cynoglossus,* 15.89%), cunner (*T. adspersus,* 15.70%), Atlantic cod (*G. morhua,* 6.97%), yellowtail flounder (*L. ferruginea,* 6.52%) and American plaice (*H. platessoides,* 4.90%),as the species primarily responsible for the differences between the two assemblages. These species cumulatively explain 49.98% of the dissimilarity between the assemblages present during the 1980's and the post- 1992 assemblage; with all of these species occurring in lower average abundances in the post-1992 period than during the 1980's.

ANOVA comparison of the pre- and post- 1992 groupings showed significant difference in diversity $F(2,131) = 14.153$; $p<0.001$, but not in richness $F(2,131) = 2.440$; $p > 0.05$. This outcome suggests that although similar numbers of species were

still present before and after 1992, that species dominance changed and that species were less evenly distributed post-1992.

Trinity Bay – June (1982-1986, 2002)

Multi-dimensional scaling plots and group-average cluster analysis of Trinity Bay June data (1982-1986 and 2002) identified two main groups, one comprised primarily of stations from 1982-1986 and the other comprised mainly of stations from 2002 (Figure 3-9). SIMPER analysis on year groupings showed that during the 1980's Atlantic cod (*G. morhua*) were consistently in greater abundance than in the year 2002, making this species the primary discriminator. The analysis of similarity (ANOSIM) showed significant difference between groups (Global $R = 0.253$; $p = 0.001$). All of the comparisons between groups showed difference at a significance level of 0.1%.SIMPER analysis on the two groups identified by cluster analysis identified seven discriminating species. Atlantic cod *(G. morhua)*, pollock (*Pollachius virens)*, radiated shanny (*U. subbifurcata)*, Atlantic herring (*C. harengus*), rock gunnel (*Pholis gunnellus*), American plaice (*H. platessoides*), and snailfish (*Liparis* spp.) (Table 3-2) accounted for 91.89% of the dissimilarity between the two groups.

ANOVA showed significant differences in Shannon-Wiener diversity $F(1,336) = 64.737$; $p < 0.001$ and richness $F(1,336) = 62.087$; $p < 0.001$ between the 1980's group and the 2002 group. This outcome is in agreement with the conclusion that the community composition of ichthyoplankton in Conception and Trinity Bay changed from a more diverse species rich community in the 1980's to a less diverse and less

species rich community after the early 1990's.

Trinity Bay – July (1982-1986, 1997, 2002)

Multi-dimensional scaling plots and group average cluster analysis of Trinity Bay July data (1982-1986, 1997 and 2002) resulted in the classification of two main groups, one that included 1982-1986 and another that grouped data from 1997 and 2000 (Figure 3-10). The analysis of similarity (ANOSIM) showed significant difference between groups (Global $R = 0.304$; $p = 0.001$). All of the comparisons between groups showed difference at a significance level of 0.1%.SIMPER analysis of the two groups designated by cluster analysis identified capelin (*M. villosus,* 20.17%), American plaice (*H. platessoides,* 10.52%), radiated shanny (*U. subbifurcata,* 10.32%), Atlantic cod (*G. morhua,* 9.14%), and snailfish (*Liparis* sp., 6.83%) as the top five discriminating species, accounting for 56.97% of the dissimilarity between groups. In contrast to the pattern observed in the Conception Bay July data, not all species identified by SIMPER analysis were more abundant in the 1982-1986 stations than in the 1997/2002 stations. Indeed, cunner, Atlantic herring, yellowtail flounder, Arctic shanny, sculpins and *Lumpenus* spp were more abundant in 1997/2000 than in previous years (Table 3-3). In contrast, *Liparis* spp. and radiated shanny decreased less than 30% from their pre-1992 abundances. Of the species that showed relatively low declines or increases in abundance, only yellowtail flounder and Atlantic herring are fished commercially or susceptible to bycatch loss.

ANOVA showed significant difference in species diversity $F(1,493) = 21.176$; p

<0.001 and richness $F(1,493) = 17.539$; p <0.001 between the 1982-86 and 1997/2000 groups. However, in contrast to the patterns observed in Conception Bay (June-August) and in June, mean diversity and richness were both higher in the 1997/2002 group than in the pre-1992 group.

Trinity Bay – August (1982-1986, 2002)

Multi-dimensional scaling plots and group-average cluster analysis of Trinity Bay August data (1982-1986 and 2002) identified two main groups, one that included all of the years from 1982-1986 and another that contained only the year 2002 (Figure 3-11). The analysis of similarity (ANOSIM) showed significant difference between groups (Global $R = 0.319$; $p = 0.001$). All of the comparisons between groups showed difference at a significance level of 0.1%.SIMPER analysis of the two groups designated using group-average cluster analysis identified American plaice (*H. platessoides,* 19.01%), Atlantic cod (*G. morhua,* 15.28%), witch flounder (*G. cynoglossus,* 14.77%), cunner (*T. adspersus,* 14.52%), and capelin (*M. villosus,* 11.58%) as the top five discriminating species accounting for 75.16% of the dissimilarity between groups. Redfish and cunner were the only species that were more abundant in the year 2002 grouping, whereas other species were more abundant in the 1982-1986 group.

ANOVA showed significant difference in species diversity $F(1,334) = 62.219$; p <0.001 and richness $F(1,334) = 95.690$; p <0.001 between the 1982-86 and 2002 groups. This outcome is consistent with the conclusion that the community

composition of ichthyoplankton in Conception and Trinity Bays changed from a more diverse species rich community in the 1980's to a less diverse and less species rich community after the early 1990's.

Seasonal Comparisons of Shannon-Wiener Diversity, Richness and Abundance

Placentia Bay (1997-1999)

Mean monthly and yearly Shannon-Wiener diversity increased between the months of June and August with no clear pattern present during the month of April and no clear seasonal trend in Shannon-Wiener diversity (Figure 3-12). Yearly Shannon-Wiener diversity also increased from 0.44 in 1997 to 0.75 in 1999 (Figure 3-13). Monthly means of species richness in June increased from 1.9 in 1997 to 4.1 in 1999 (Figure 3-14). However, no patterns in species richness were evident during the months of April or August, nor were any patterns in species richness evident among years (Figure 3-13). Monthly mean abundances were low during the months of April and June with no clear pattern present during either of these months. During the month of August monthly mean abundance was much higher and showed a decline from ~1319 larvae·1000m^{-3} in 1997 to ~371 larvae·1000m^{-3} in 1999 (Figure 3-15).

Conception Bay (1985-1998)

Plots of mean monthly Shannon-Wiener diversity showed a decrease from July to August with no clear pattern present during the month of June in Conception Bay (1985-1998) (Figure 3-16). Monthly means of species richness showed a slight decrease from July to August by approximately 1-2 species (Figure 3-17). However,

an increase in species richness occurred during the month of June in 1990 when compared to 1985 and 1986 (Figure 3-17). Mean total abundance showed a sharp drop in the early 1990's when compared to abundances during the mid 1980's (Figure 3-18). During July 1997 there appeared to be a sharp increase in abundance relative to previous years. However, the July 1997 data were limited in spatial coverage because they were collected as part of a patch study and may therefore not reflect average abundance throughout the bay. In this analysis, commercial and non-commercial species were both more abundant pre-1992 than post-1992 (Table 3-4).

Trinity Bay (1982-2002)

Plots of mean monthly Shannon-Wiener diversity for Trinity Bay indicate a summer peak in diversity in July with lower values during the months of June and August (Figure 3-19). Monthly means of species richness were slightly lower in June and August than in July (by approximately 1 species, Figure 3-20). Mean total abundance was greater during June, July and August of the 1980's relative to the late 1990's and early 2000's (Figure 3-21).

Composite figures of mean Shannon-Wiener diversity, mean species richness, and total abundance for Trinity, Conception and Placentia Bays during the months of June, July or August showed no consistent pattern in Shannon-Wiener diversity or species richness through time (Figure 3-22), with the exception of a modest decline in species richness after 1992 in Conception Bay (Figure 3-23). Total abundance did decline;

however, in 1992 in both Trinity and Conception Bays (Figure 3-24).

iv. Discussion

The most striking trend observed in these analyses is the significant difference between the larval fish communities present before and after the Newfoundland groundfish collapse in 1992. Larval concentrations for commercial groundfish species decreased in abundance in the early 1990s and have not recovered since, whereas non-commercial species that disappeared during the same period generally showed smaller declines and, in some instances, increased in abundance after 1994 (Table 3-3, Table 3-4). Arctic cod, which were present in Newfoundland waters during the time of the fisheries collapse in 1991-1994, did not persist beyond these years, indicating that their presence in the region may have been associated with cooler-than-average water temperatures (Figure 3-7, Figure 3-25). Non-commercial species such as cunner, *Liparis* spp., and *Lumpenus* spp., which are not susceptible to commercial fishing bycatch, were among the few species whose abundances post-1992 were equivalent to or greater than those observed during the years prior to 1991. Additional non-commercial species such as Arctic shanny maintained a slightly greater abundance post- 1992 in addition to their increased abundance during a cold period in 1991-92 (Figure 3-25). Radiated shanny also maintained relatively constant abundance post 1992, with relatively small variations in abundance.

Inter-annual Variability

Drinkwater (1996) described the 1980's as on average, the coldest decade recorded

since data collection began in the 1940's, and he also identified an approximately decadal temperature oscillation whose presence was established in 1960. Recognition of this decadal oscillation resulted in the identification of temperature lows in the early 1970's, 1980's and 1990's (Drinkwater, 1996). Taggart at al. (1994) affirm that recruitment of cod (*G. morhua*) was negatively affected by anomalous cold from 1983 through 1994 (the year in which their study was published), with only brief warming in 1986 and 1987. The largest deviation from average temperatures during the cooling period of the 1980's and early 1990's was in early summer 1991, when water temperatures were a record 3°C below average (Colbourne et al., 1997).

This study does not incorporate an analysis of temperature data and I am therefore unable to quantitatively establish a statistically valid connection between the declines in larval abundances and the reduction in species diversity that occurred after the early 1990's to temperature variations that have been documented during the same time period. Nonetheless, the data presented in Tables 3-3 and 3-4 that shows differences in the declines and recoveries of commercial and non-commercial species is strongly suggestive that factors other than commercial fishing also contributed to some of the changes in community composition that occurred within Newfoundland embayments from the 1980s through 2002. Future analysis of hydrographic data could help to clarify whether temperature was an important factor.

These results demonstrate an important pattern with respect to issues of potential gear differences. Conception Bay data sets from both 1985 and 1986 were collected using

ring nets whereas data collected in 1990 were collected using Tucker Trawls. The temporal patterns observed for Conception Bay are evident despite dissimilarity in gear type that would tend to dampen the pattern. Importantly, previous studies have shown that Tucker trawls produce higher estimates of diversity and abundance than do nets that filter smaller water volumes (Pepin and Shears, 1997). Therefore, if there is an effect of gear, then the temporal change reported here is likely an underestimate (Carter, unpub. data), in that gear bias alone would have produced a pattern opposite to that reported here (i.e. the 1990 abundances and diversity should be higher because they were collected with Tucker trawls). The presence of the change in community composition is also apparent in the Trinity Bay data (Figures 3-9, 3-10 and 3-11). Different mesh sizes were used during the earlier collections than for 2002, which would tend to decrease similarities with all of the earlier collections. Again, despite the differences in gear, similarities were observed between the larval communities through the pre- and post- 1992 periods but communities differed during the period around 1992.

The Conception Bay July data also suggest that temperature or a related environmental variable has played a role in changes in larval fish composition during the time of the fisheries collapse in Newfoundland. The data indicates that at the time adult fish were moving away from the northern reaches of their distributions to the edges of the continental shelf and adult biomass was declining to extremely low levels in the inshore (Gomes, 1995), abundances of historically more abundant larvae such as capelin and cunner were declining (Figure 3-3 and Figure 3-4). Additionally, arctic

and winter species such as Arctic cod and Arctic shanny became more abundant in the 1991-1994 summer community (Figure 3-7).

The decline in diversity and richness of the larval community observed in Conception Bay occurred during the same period that the record temperature low was observed on the Newfoundland shelf in 1991 (Colbourne et al., 1997; Fig. 3-25). A causal relationship between larval diversity and richness cannot be determined without further analysis, however, it can be concluded that based on the larval fish assemblages, the groundfish of the inshore Newfoundland waters experienced a drastic change in community composition that coincided with the years of the groundfish collapse. This collapse negatively affected all of the larval taxa collected in this study with the exception of Arctic cod, which temporarily increased in the Newfoundland inshore. This result suggests that further investigation into environmental affects is needed as temperature may also have contributed to the collapse of groundfish, given that effects extended beyond commercially-targeted species. The results of the annual ANOVAs, cluster analysis and the MDS of Trinity Bay July and August data provide support that a change in the composition of larval fish from pre- to post- 1991-1994 did occur. August data from Conception Bay are consistent with the patterns described above, and illustrate the shift in community composition more clearly than any of the other Conception Bay data (Figure 3-8). The August analysis excludes the anomalous years of 1991 and 1992 (characterized by very low larval abundances, presence of winter species and arctic species in July) and therefore shows a more obvious change in species composition of the historically abundant species from pre- to post-1992

(Table 3-5).

Overexploitation of Fish Stocks and Groundfish Recovery

It is widely accepted, that the groundfish stocks of the northwest Atlantic were heavily overexploited during the period commencing in the 1960's up until the time of the groundfish collapse in the early 1990's (Hutchings and Myers, 1994; Taggart et al., 1994; Myers and Cadigan, 1995; Hutchings, 1996; Hutchings and Ferguson, 2000; Rose, 2003). There has been considerable scepticism regarding the effects of environmental factors in the collapse of the fisheries (Hutchings and Myers, 1994; Myers and Cadigan, 1995). Although environmental variation has been dismissed as the primary contributing factor in the collapse of the groundfish the unusual cold period that preceded the collapse may have increased the vulnerability of the stock to overfishing. The larval data presented here suggest that populations of multiple species, including taxa that are not targeted by commercial fisheries, changed significantly during the early 1990's and raises the question as to whether cooler temperatures may have led to an increase in arctic species in more southerly regions. The data presented here suggests that the presence of Arctic and winter species did not persist beyond the early 1990's. The data further suggest that species not susceptible to commercial fishing have shown lesser declines or in some cases increased in abundance. Thus, further analysis of hydrographic data could help to tease out causal relationships. A very plausible explanation for the changes in the larval community is that overfishing, combined with poor enrivonmental conditions, resulted in a clear decline in eggs and larvae groundfish and non-targeted taxa during the early 1990s and

a corresponding increase in species that favoured colder conditions. In the case of the non-targeted taxa, many species were able to rebound once environmental conditions improved but because overfishing had reduced groundfish stocks to such low levels there was no recovery when conditions improved.

Seasonal Patterns

Data collected in this study suggest that the abundance of larval fish in the inshore Newfoundland waters closely track the well-established seasonal pattern of Northwest Atlantic environmental variability (Petrie et al., 1991; Colbourne, 2004). These findings lend support to the finding of Methven et al. (2001) who found that estuarine species collected in Trinity Bay, Newfoundland exhibited seasonal clustering analogous to the groupings found here. The results presented here echo Methven et al. (2001), who concluded that the seasonal variations in the inshore fish community is greater than annual variation in structuring the fish assemblages. Additionally, Methven et al. (2001) described seasonal transition communities, which was also evident in the larval data presented here.

v. Lack of Groundfish Recovery

Many possibilities have been proposed to explain the lack of recovery of groundfish since the moratorium began in 1992. This study raises some questions regarding the abundances and survival of larvae of commercially targeted versus non-commercially targeted species and what role environment may have played in their declines. I provide evidence that the diversity, abundance, and richness of the larval communities changed in association with the collapse of groundfish during the early 1990s. Further

analysis of environmental data is required, however. Rose (2003) suggests that pulse fisheries exploit strong year classes before fish have an opportunity to re-establish their numbers, thereby suppressing recovery in the region. In addition, by catch from ongoing commercial fisheries that target more abundant species, combined with unreported catches have possibly affected abundance of groundfish more so than non-commercial species that often occupy habitats that are not vulnerable to fishing and bycatch pressure. Thus, a simple lack of adult spawners is likely the primary reason for the absence of a recovery of groundfish. Alternative trophic interactions in the form of an invertebrate/vertebrate regime shift may also be impeding recovery (Rose, 2003; Frank et al., 2005) or an alternative steady state within the ecosystem may have been reached similar to that described for anchovy and sardines within the Pacific Ocean (Chavez et al., 2003). Stock health and reduced age of maturity (Taggart et al., 1994) are further compounding factors that may be hampering egg and larval survival. It is likely that some combination of these factors have interacted to hinder recovery of the northern cod stock. The results presented here suggest that substantial changes occurred in the ichthyoplankton community during the cold period of the early 1990s. Clearly overfishing contributed to the patterns observed in groundfish larvae, but this time period also resulted in substantial changes in non-commercial species that were less vulnerable to bycatch mortality. Importantly, many of the non-commercial species that changed in the early 1990s were able to quickly recover when conditions presumably became more favourable. The most likely explanation for the differences in response of commercial and non-commercial species is that overfishing had pushed groundfish populations to extremely low levels and the additional insult of a period of

harsh environmental conditions added further to this decline. Groundfish population levels were therefore too low to allow recovery, unlike the situation for non-commercial species. The changing nature of ichthyoplankton assemblages during this critical period therefore reflects a combination of fishing impacts and environmental conditions.

vi. Literature Cited

Bradbury, I.R., P.V.R. Snelgrove and S. Fraser (2000) Transport and development of eggs and larvae of Atlantic cod, *Gadus morhua*, in relation to spawning time and location in coastal Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences. 57: 1761 – 1772.

Bradbury, I. R., P.V.R. Snelgrove and P. Pepin (2003) Passive and active behavioural contributions to patchiness and spatial pattern during the early life history of marine fishes. Marine Ecology Progress Series. 257: 233-245.

Caldeira, R.M.A. (2002) Multidisciplinary oceanographic studies of a small island in the Southern California Bight. PhD Thesis. University of California. Los Angeles.

Carscadden, J.E. (2005) Did signals from seabirds indicate changes in capelin biology during the 1990s? - comment on Davoren & Montevecchi. Marine Ecology-Progress Series 285: 289-297.

Chavez, F.P., J. Ryan, S.E. Lluch-Cota and M. Niquen C. (2003) From Anchovies to Sardines and Back: Multidecadal Change in the Pacific Ocean. Science. 299: 217-221.

Clarke, KR (1993). Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clarke, K.R. and R.M.Warwick (1994) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, Natural Environment Research Council, Plymouth, UK (1994) 144 pp

Clarke, K.R. Somerfield, P.J. and M.G. Chapman (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. Marine Biology and Ecology 330: 55-80.

Colbourne, E., S. Narayanan and S. Prinsenberg (1994) Climateic changes and environmental conditions in the Northwest Atlantic, 1970-1993. ICES Marine

Science Symposia 198: 311-322.

Colbourne, E., B. deYoung, S. Narayanan and J. Helbig (1997) Comparison of hydrography and circulation on the Newfoundland Shelf during 1990-1993 with the long-term mean. Canadian Journal of Fisheries and Aquatic Sciences. 54 (Suppl.1): 68-80.

Colbourne, E. B. (2004) Decadal Changes in the Ocean Climate in Newfoundland and Labrador Waters from the 1950's to the 1990's. e-Journal of Northwest Atlantic Fishery Science. V34, art. 4. Available from http://journal.nafo.int/34/colbourne/colbourne-main.html [accessed 18 January 2006].

Craig, J.D.C and E.B. Colbourne (2002) Trends in stratification on the inner Newfoundland shelf. Canadian Science Advisory Secretariat Research Document 2002/071. 15pp.

Davidson, F. J. M., Greatbatch, R. J. and de Young, B. (2001) Asymmetry in the response of a stratified coastal embayment to wind forcing. Journal of Geophysical Research 106: 7001-7015.

Department of Fisheries and Oceans Statistical Services (2005) Updated 2004-07-06 http://www.dfo-mpo.gc.ca/communic/statistics/commercial/landings/index_e.htm

deYoung, B. and B. Sanderson (1995) The Circulation and Hydrography of Conception Bay, Newfoundland. Atmosphere-Ocean. 33: 135-162.

deYoung, B. R. Peterman, A.R. Dobell, E. Pinkerton, Y. Breton, A.T. Charles, M.J. Fogarty, G.R. Munro and C.T. Taggart (1999) Canadian marine fisheries in a changing and uncertain world. A report prepared for the Canadian Global Change Program of the Royal Society of Canada. Canadian Special Publication of Fisheries and Aquatic Sciences Number 129.199p.

Dickson, R.R., J. Meincke, S-A. Malmberg and A.J. Lee (1988) The "Great Salinity Anomaly" in the Northern North Atlantic 1968-1982. Progress in Oceanography 20: 103-151.

Drinkwater, K. F. (1996) Atomostpheric and Oceanic Variability in the Northwest Atlantic During the 1980's and Early 1990's. Journal of Northwest Atlantic Fisheries Science 18: 77-97.

Drinkwater, K.F., E. Colbourne and D. Gilbert (2001) Overview of Environmental Conditions in the Northwest Atlantic in 2000. NAFO SCR Doc. 01/36, 20 pp.

Drinkwater, K.F. and D. Gilbert (2004) Hydrographic Variability in the Waters of the Gulf of St. Lawrence, the Scotian Shelf and the Eastern Gulf of Maine (NAFO Subarea 4) During 1991-2000. e-Journal of Northwest Atlantic Fishery Science.

Vol. 34, art. 6. Available from http://journal.nafo.int/34/6-drinkwater.html

Field, J.G., K.R. Clarke & R.M. Warwick (1982) A practical method for analyzing multispecies distribution patterns. Marine Ecology Progress Series 8:37-52.

Frank, K. T., J.E. Carscadden and J.E. Simon (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Canadian Journal of Fisheries and Aquatic Sciences. 53: 1473-1486.

Frank, K.T. and W.C. Leggett (1983) Multispecies larval fish associations: accident or adaptation? Canadian Journal of Fisheries and Aquatic Sciences. 40:754-762.

Frank, K.T., B. Petrie, J.S. Choi and W. C. Leggett (2005) Trophic Cascades in a Formerly Cod-Dominated Ecosystem. Science. 308: 1621-1623.

Gerasimova, O.V. and V. M. Kiseleva (1998) Long-term Variations in Cod Distribution and Feeding on the Newfoundland Shelf in Spring and Summer. North Atlantic Fisheries Organization Science Council Studies. 31: 79–110.

Gomes, M.C., R.L.Haedrich and M.G. Villagarcia (1995) Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador shelf, north-west Atlantic, 1978-1991. Fisheries Oceanography. 4: 85-101.

Harris, L. (1990) Independent review of the state of the northern cod stock. DFO Rep. No. 4379. Department of Fisheries and Oceans, Ottawa, Ont.

Helbig, J, G. Mertz and P. Pepin (1992) Environmental influences on the recruitment of Newfoundland/Labrador cod. Fisheries Oceanography.1(1):39-56.

Hutcheson, K. (1970) A test for comparing diversities based on the Shannon formula. Theoretical Biology 29: 151-154.

Hutchings, J.A. and R.A. Myers (1994) What can be learned from the collapse of a renewable resource? Atlantic Cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences. 51:2126-2146.

Hutchings, J.A. (1996) Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Canadian Journal of Fisheries and Aquatic Sciences 53: 943-962.

Hutchings, J.A. and M. Ferguson (2000) Temporal changes in harvesting dynamics of Canadian inshore fisheries for northern Atlantic cod, *Gadus morhua.* Canadian Journal of Fisheries and Aquatic Sciences. 57:805-814.

Lilly, G. R., and J. E. Carscadden. (2002) Predicting the Future of Marine Fish and Fisheries Off Labrador and Eastern Newfoundland under Scenarios of Climate Change: Information and Thoughts for the Arctic Climate Impact Assessment (ACIA). Department of Fisheries and Oceans Canada (DFO) Canadian Science Advisory Secretariat (CSAS) Research Document 2002/111; Public Works and Government Services Canada; [online] http://www.dfo-mpo.gc.ca/csas/Csas/DocREC/2002/RES2002_111.pdf

Maillet, G.L. and P. Pepin (2005) Timing of Plankton Cycles on the Newfoundland Grand Banks: Potential Influence of Climate Change. NAFO SCR Doc. 05/12, 12 pp.

Magurran, A.E. (2004) Measuring Biological Diversity. Blackwell Publishing. Maldan, MA.(2004) 268pp.

Methven, D. A., R. L. Haedrich and G.A. Rose (2001) The Fish Assemblage of a Newfoundland Estuary: Diel, Monthly and Annual Variation. Estuarine, Coastal and Shelf Science. 52: 669-687.

Myers, R.A. and N.G. Cadigan (1995) Was an increase in natural mortality responsible for the collapse of northern cod? Canadian Journal of Fisheries and Aquatic Sciences. 52:1274-1285.

Parsons, L.S. and W.H. Lear (2001) Climate variability and marine ecosystem impacts: a North Atlantic perspective. Progress in Oceanography 49, 167–188.

Pepin, P., J.A. Helbig, R. Laprise, E. Colbourne & T.H. Shears (1995) Variations in the contribution of transport to changes in planktonic animal abundance: a study of the flux of fish larvae in Conception Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences. 52:1475-1486.

Pepin, P. and T.H. Shears (1997) Variability and capture efficiency of bongo and tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. Canadian Journal of Fisheries and Aquatic Sciences. 54: 765-773.

Petrie, B., J. Loder, S. Akenhead and J. Lazier (1991) Temperature and salinity variability on the eastern Newfoundland Shelf: the annual harmonic. Atmosphere-Ocean. 29: 14-36.

Rogers, J.C. (1984) The Association between the North Atlantic Oscillation and the Southern Oscillation in the Northern Hemisphere. Monthly Weather Review.112 (10):1999–2015.

Rose, G. A., B. deYoung, D.W. Kulka, S.V. Goddard and G. L. Fletcher (2000)

Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Can. J. Fish. Aquat. Sci. 57: 644-663.

Rose, G (2003) Fisheries Resources and Science in Newfoundland and Labrador: An Independent Assessment. Royal Commission on Renewing and Strengthening our Place in Canada. 84 pp.

Rose, G. A. (2004) Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. Can. J. Fish. Aquat. Sci. 61:1553-1557.

Sneath, P.H.A. and R.R. Sokal (1973) Numerical Taxonomy. W.H. Freeman and Company, San Francisco. 573pp.

Snelgrove, P.V.R., I.R. Bradbury and S. Fraser (2008) Temporal variation in fish egg and larval production by pelagic and demersal spawners in a large Newfoundland coastal embayment. Canadian Journal of Fisheries and Aquatic Sciences. 65: 159-175.

Streiner, D.L. (1996) Maintaining standards: Differences between the standard deviation and standard error, and when to use each. Canadian Journal of Psychiatry. 41: 498-502.

Taggart, C. T. and K.T. Frank (1987) Coastal upwelling and *Oikopleura* occurrence ("Slub"): A model and potential application to inshore fisheries. Canadian Journal of Fisheries and Aquatic Sciences. 44: 1729-1736.

Taggart, C. T., J. Anderson, C. Bishop, E. Colbourne, J. Hutchings, G. Lilly, J. Morgan, E. Murphy, R. Myers, G. Rose, and P. Shelton (1994) Overview of cod stocks, Biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Marine Science Symposia. 198: 140-157.

Tian, R.C., D.Deibel, R.J. Thompson and R.B. Rivkin (2003) Modeling of climate forcing on a cold-ocean ecosystem, Conception Bay, Newfoundland. Marine Ecology Progress Series 262: 1-17.

Worm, B., M. Sandow, A. Oschlies, H. Lotze and R. A. Myers (2005) Global Patterns of Predator Diversity in the Open Oceans. Published online July 28 2005; 10.1126/science.1113399 (*Science Express* Reports) http://www.sciencemag.org /sciencexpress/recent.shtml

Yao, T. (1986) The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmosphere-Ocean. 24: 235-252.

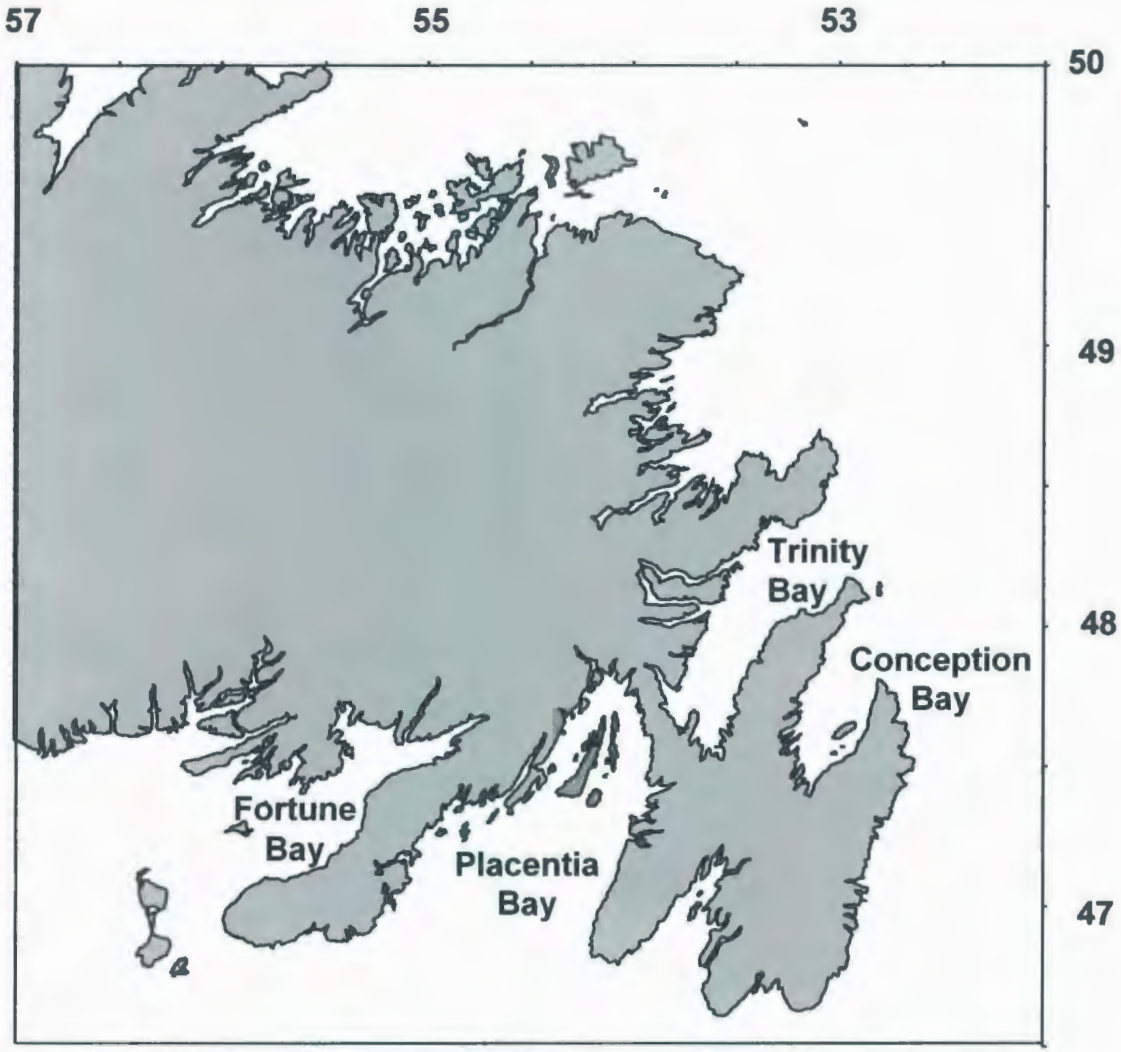

Figure 3-1: Map of eastern Newfoundland identifying coastal embayments where data collections were made, 1982 – 2002.

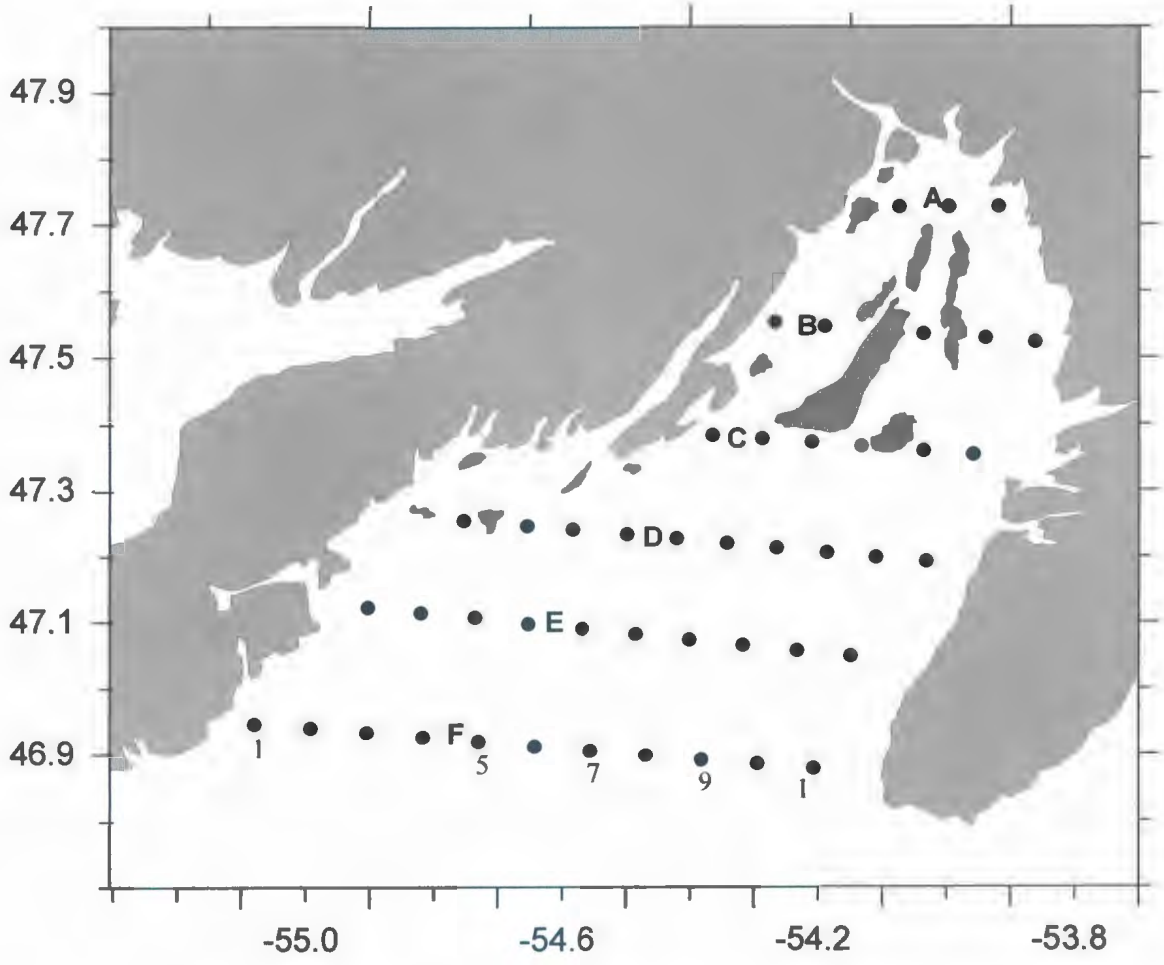

Figure 3-2: Map of Placentia Bay Fixed Sampling Grid, 1997-1999.

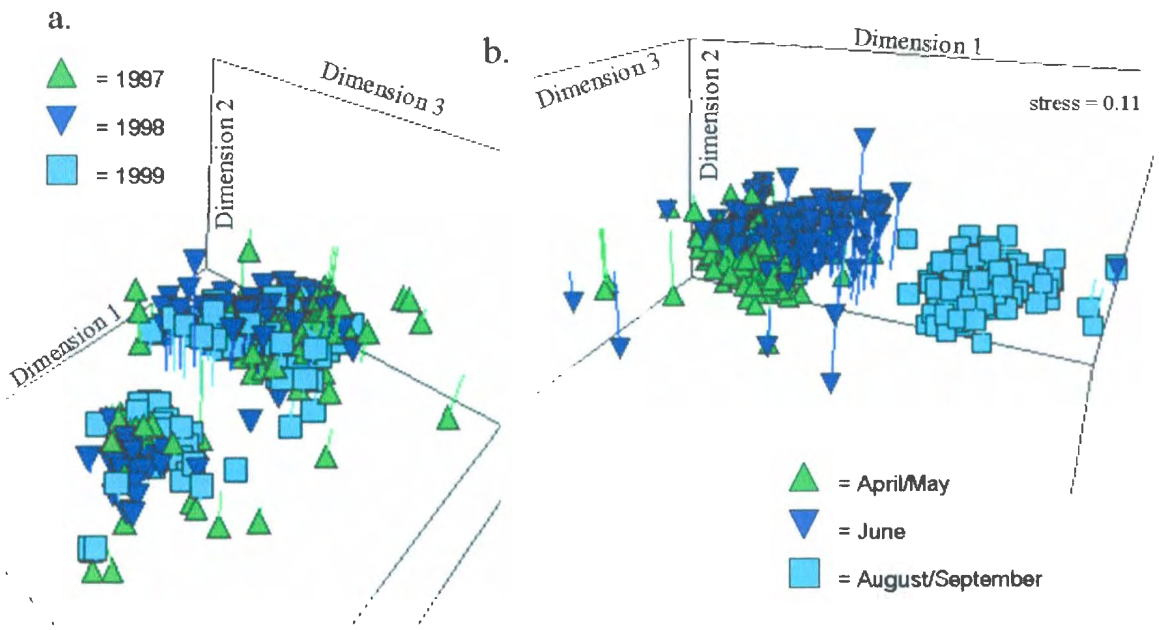

Figure 3-3: Multi-dimensional Scaling (MDS) Plots Showing Placentia Bay Data 1997-1999 a) Yearly and b) Seasonal Groupings.

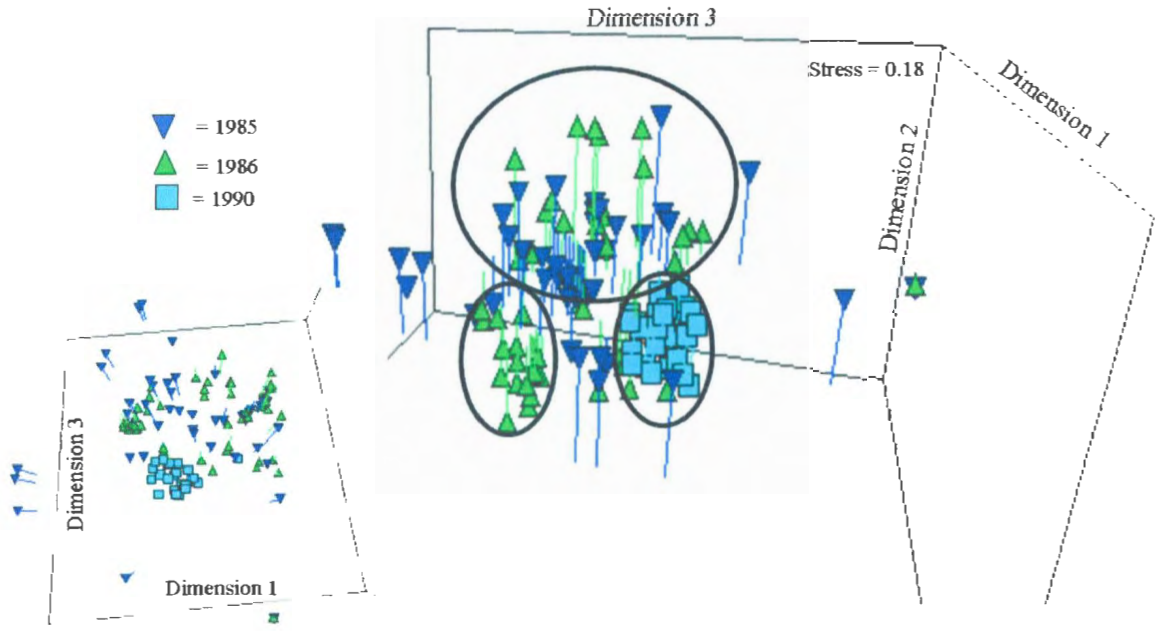

Figure 3-4: Multi-dimensional Scaling (MDS) Plots Showing Conception Bay June Data 1985-1990. Yearly groupings. Overlaid circles represent approximate classifications defined by group average cluster analysis.

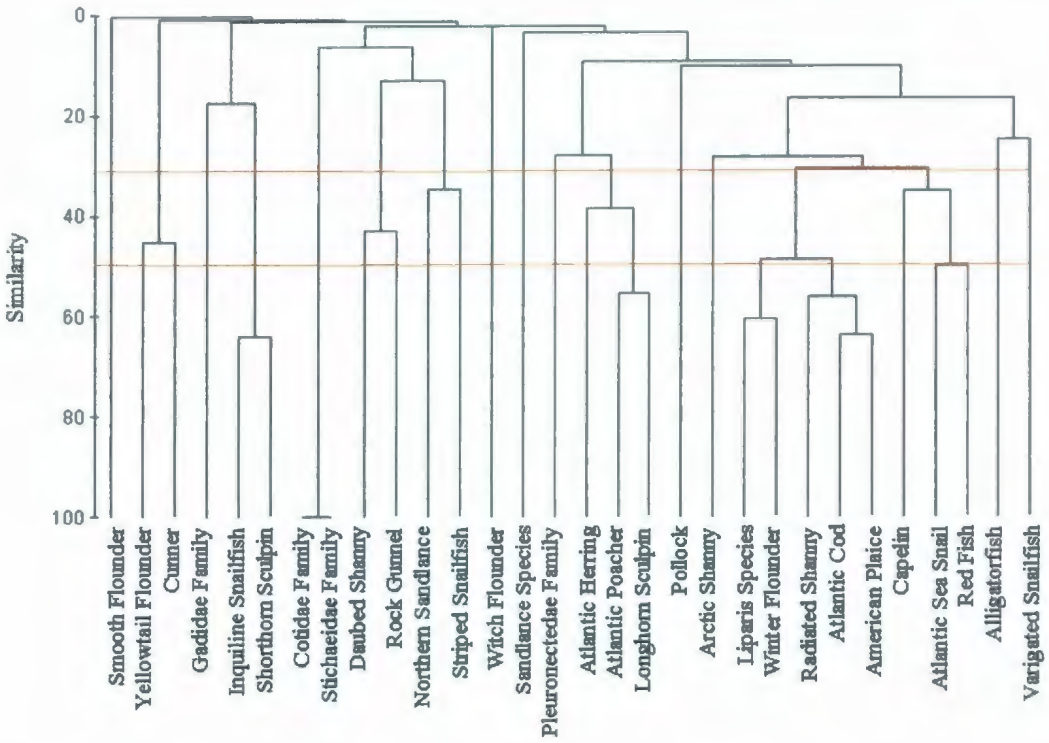

Figure 3-5: Group-average cluster plot showing Conception Bay June data 1985-1998 co-occurring species groupings. The red lines represent the similarity of co-occurring species with similarities of 30 and >50%.

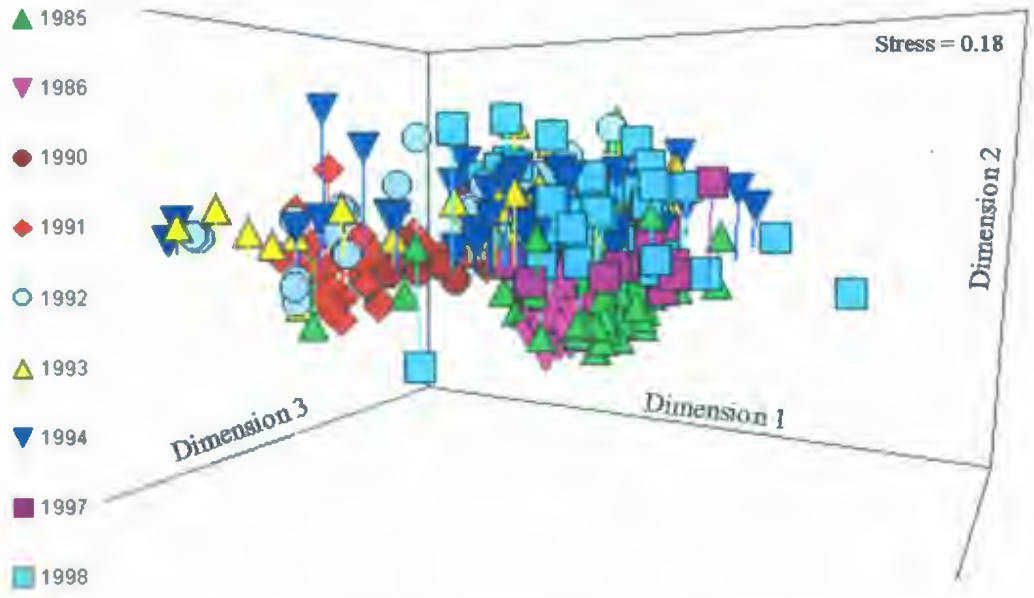

Figure 3-6a: Multi-dimensional Scaling (MDS) plot showing Conception Bay July data 1985-1998 yearly groupings.

Figure 3-6b: Multi-dimensional Scaling (MDS) Plot Showing Conception Bay July Data 1985-1998 groupings identified through group average cluster analysis.

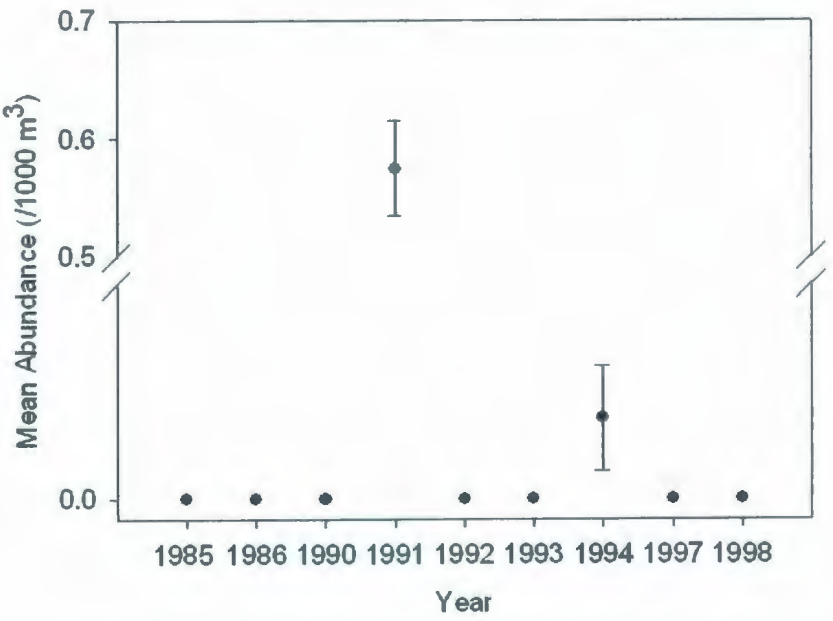

Figure 3-7: Mean abundance plot showing Arctic Cod (*Boreogadus saida)* abundance during the years 1985-1998 in Conception Bay. Bars denote standard errors.

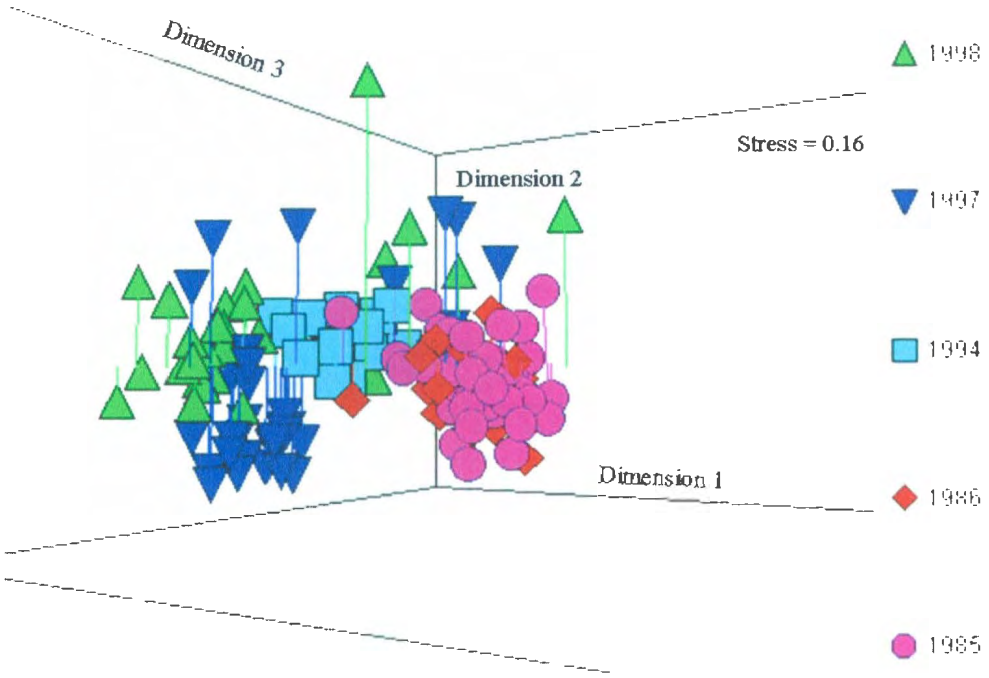

Figure 3-8: Multi-dimensional Scaling (MDS) plot showing Conception Bay August data 1985-1998 yearly groupings.

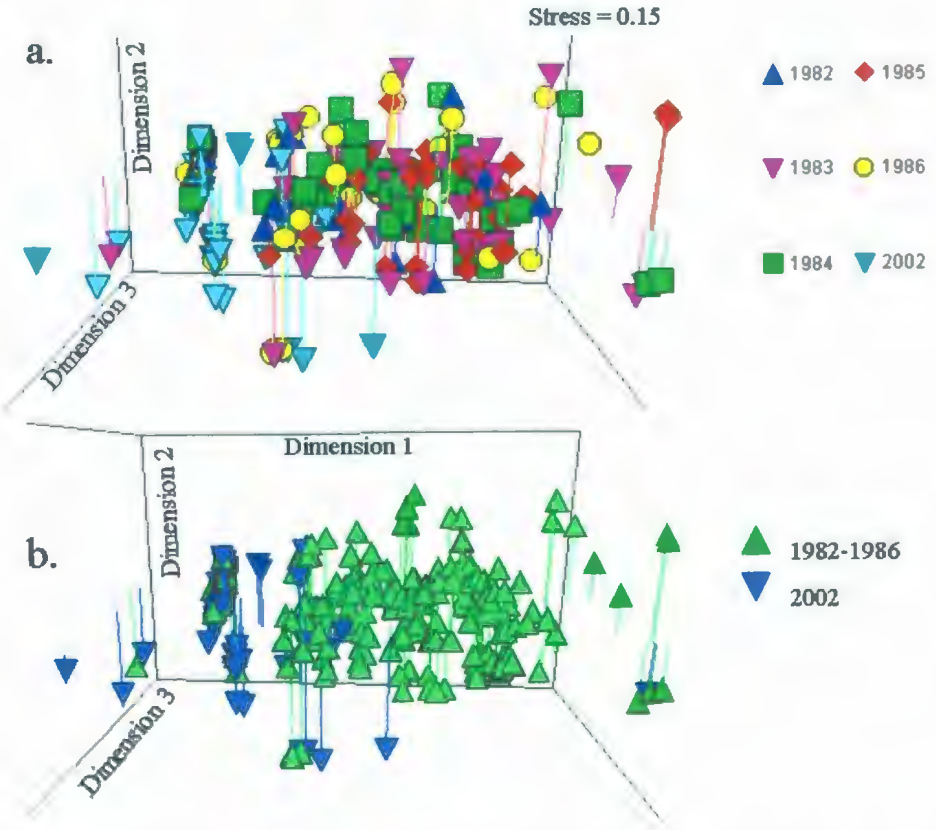

Figure 3-9: Multi-dimensional Scaling (MDS) plot showing Trinity Bay June data 1982-2002 a) Yearly groupings and b) groups identified using group average cluster analysis.

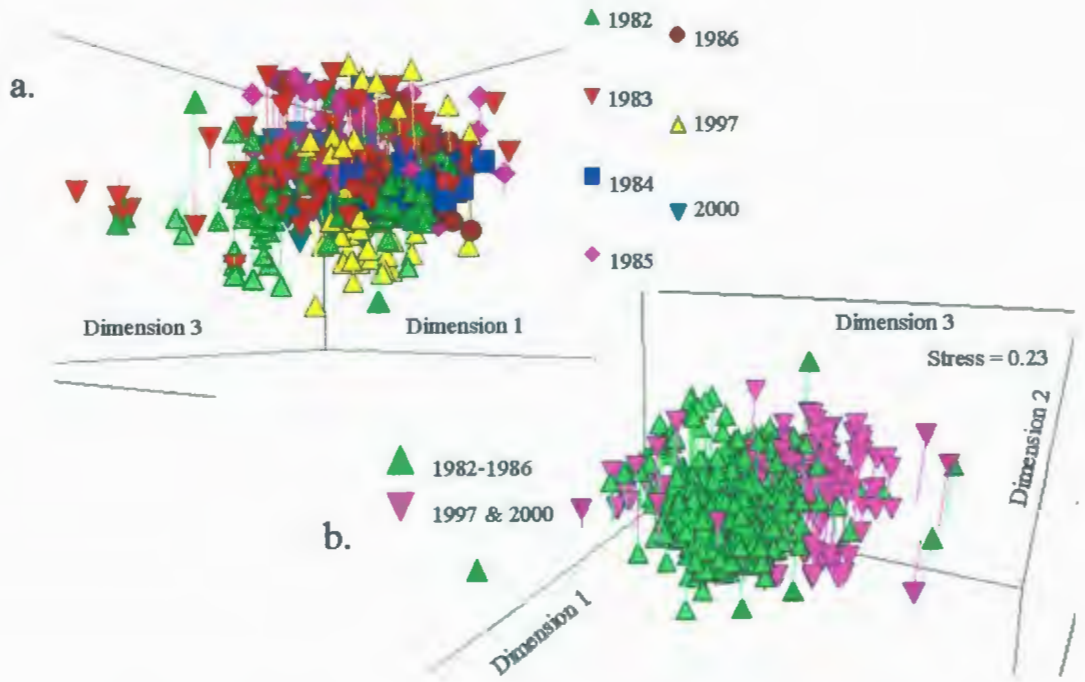

Figure 3-10: Multi-dimensional Scaling (MDS) plot showing Trinity Bay July data 1982-2000 a) Yearly groupings and b) groups identified using group average cluster analysis.

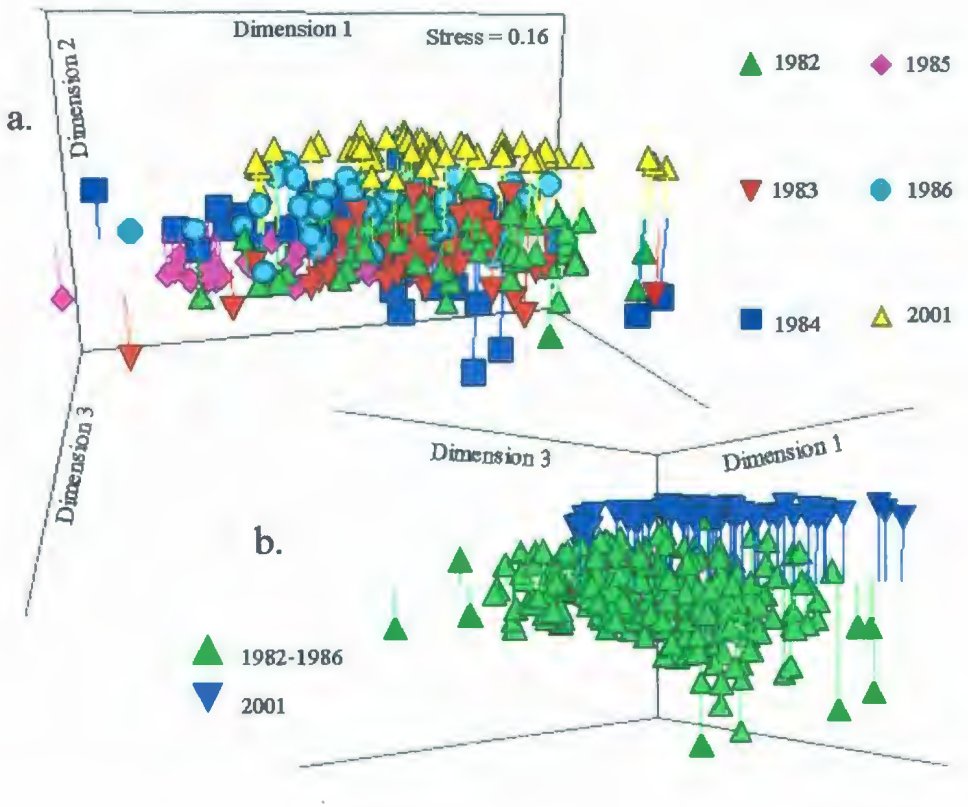

Figure 3-11: Multi-dimensional Scaling (MDS) plot showing Trinity Bay August data 1982-2000 a) Yearly groupings and b) groups identified using group average cluster analysis.

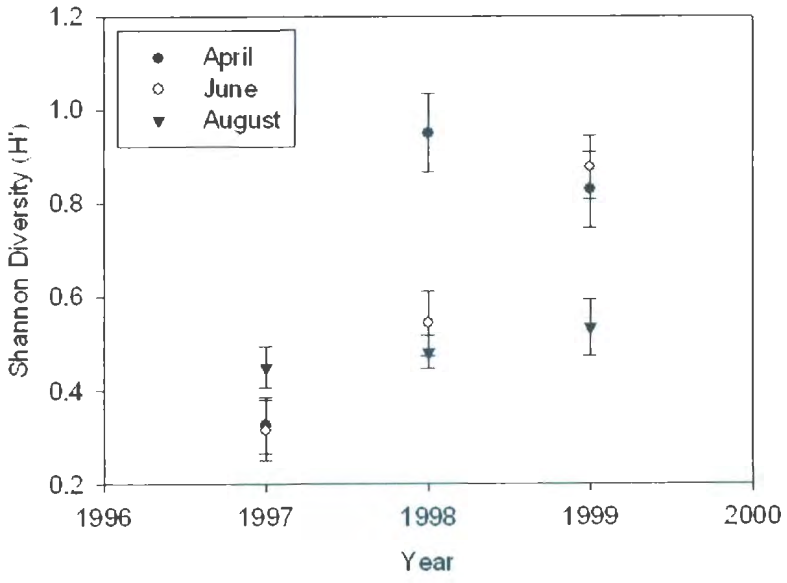

Figure 3-12: Mean Shannon Weiner Diversity in Placentia Bay 1997-1999 April – Aug. Bars denote standard errors.

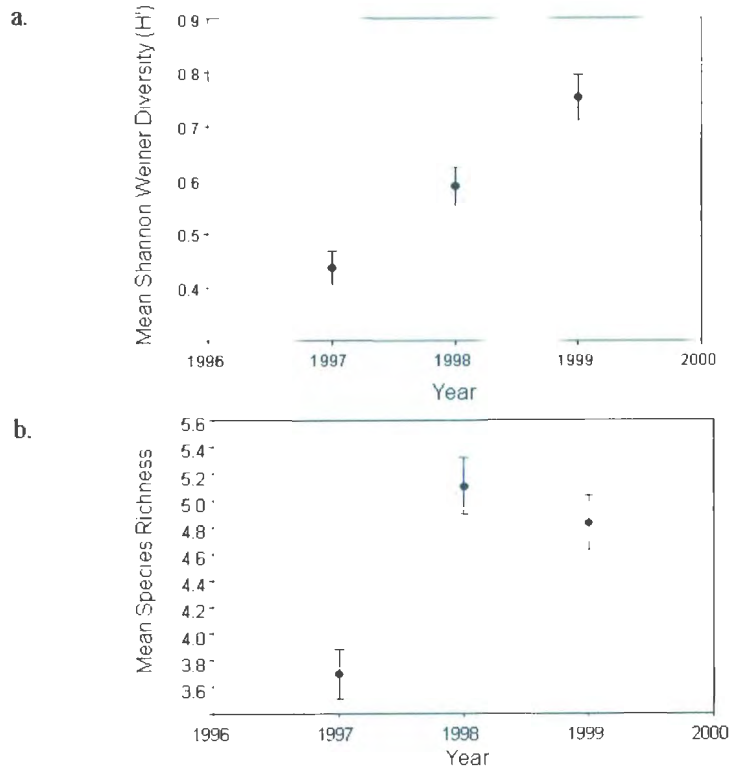

Figure 3-13: (a) Mean Shannon Weiner Diversity and (b) Species Richness in Placentia Bay 1997-1999 year totals May- August. Error Bars denote standard errors.

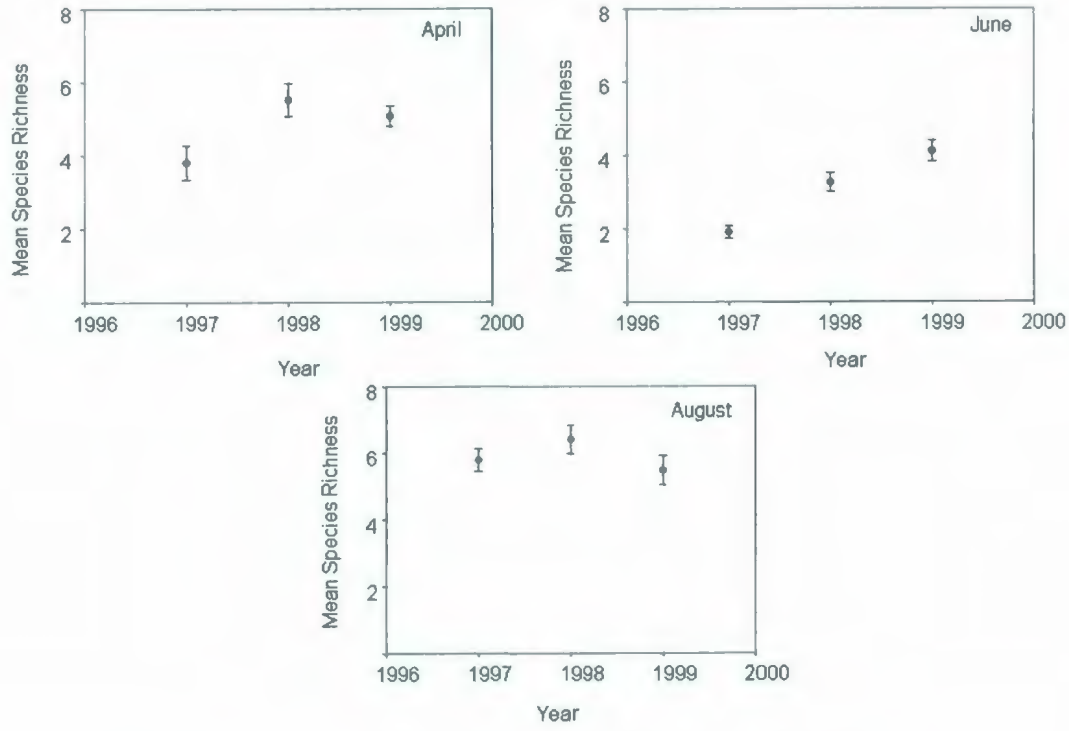

Figure 3-14: Mean Species Richness in Placentia Bay 1997-1999 April - Aug. Bars denote standard errors.

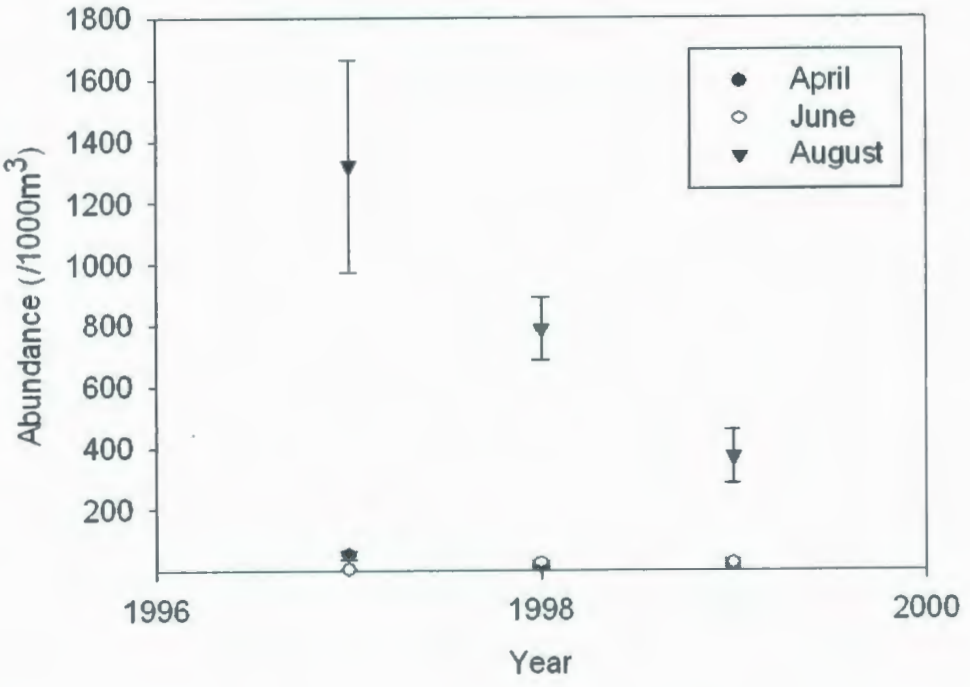

Figure 3-15: Mean Species Abundance in Placentia Bay 1997-1999 April - Aug. Bars denote standard errors.

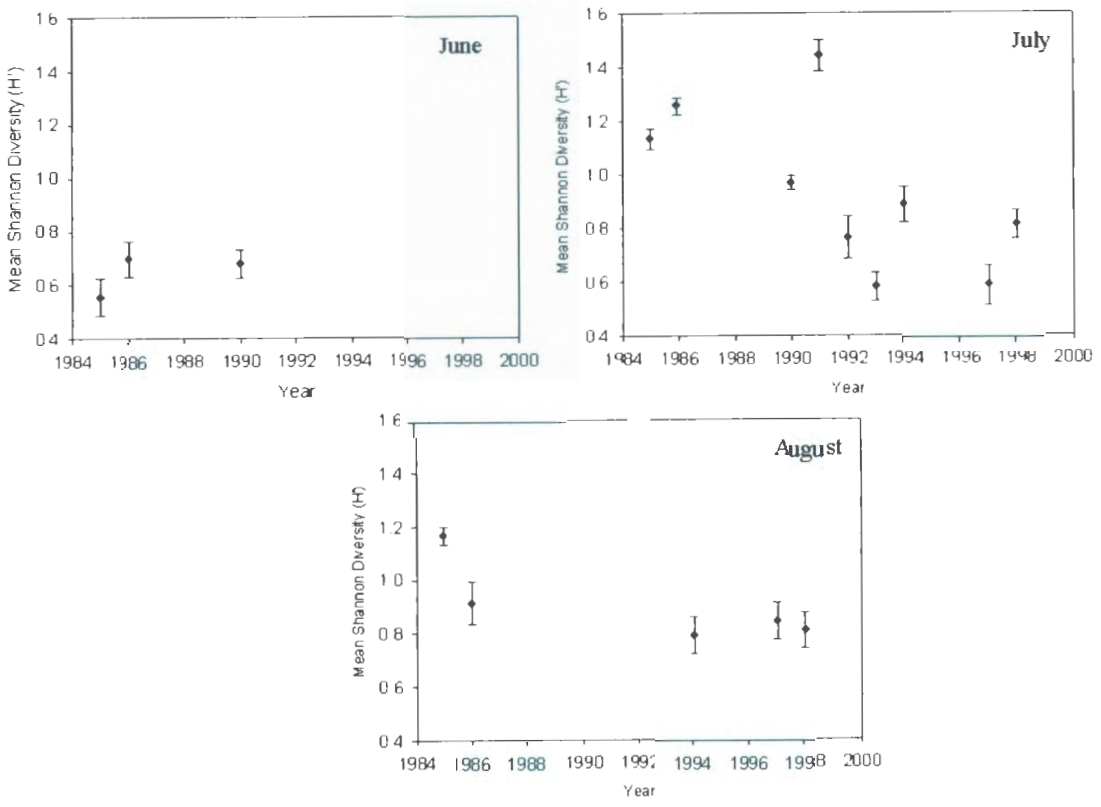

Figure 3-16: Mean Shannon Diversity in Conception Bay 1985-1998 June - Aug. Bars denote standard errors.

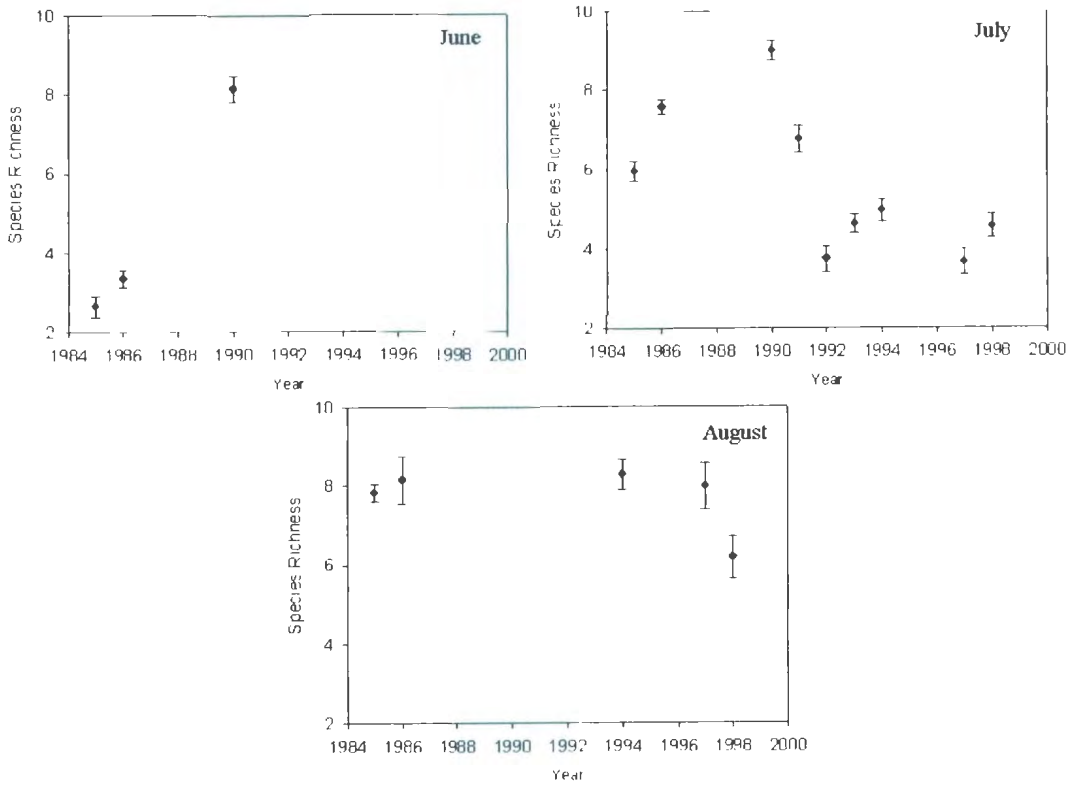

Figure 3-17: Mean Species Richness in Conception Bay 1985-1998 June - Aug. Bars denote standard errors.

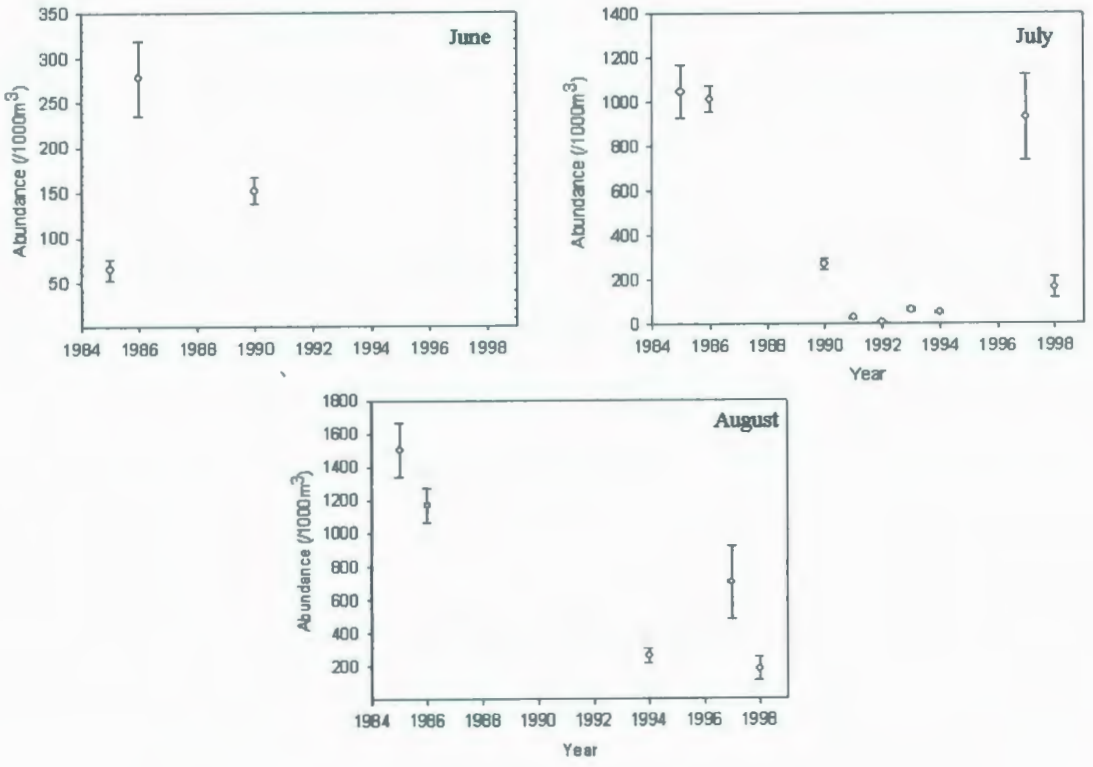

Figure 3-18: Conception Bay 1985-1998 June-Aug Mean Species Abundance. Bars denote standard errors.

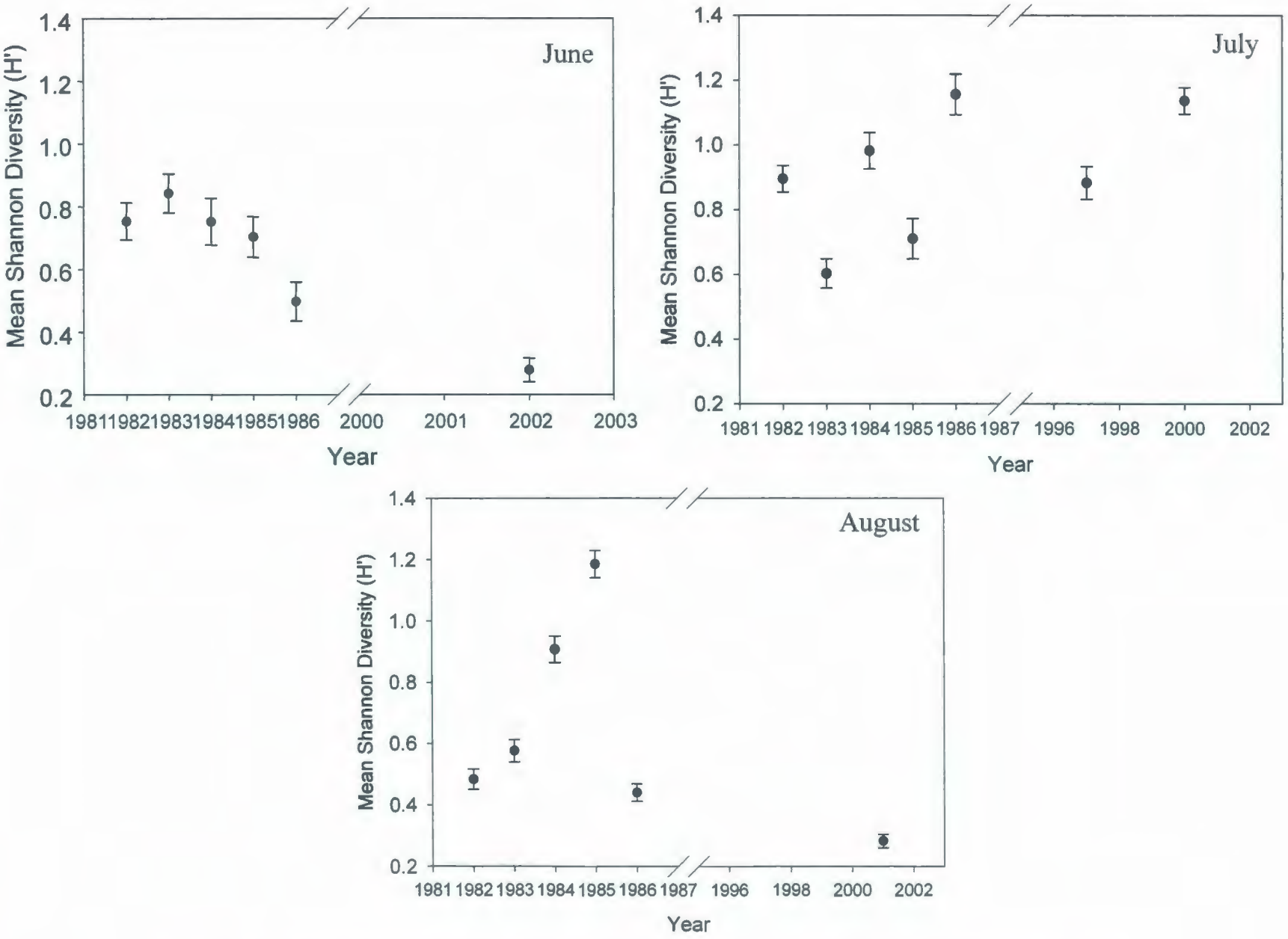

Figure 3-19: Trinity Bay 1982-2002 June-Aug Shannon Weiner Diversity. Bars denote standard errors.

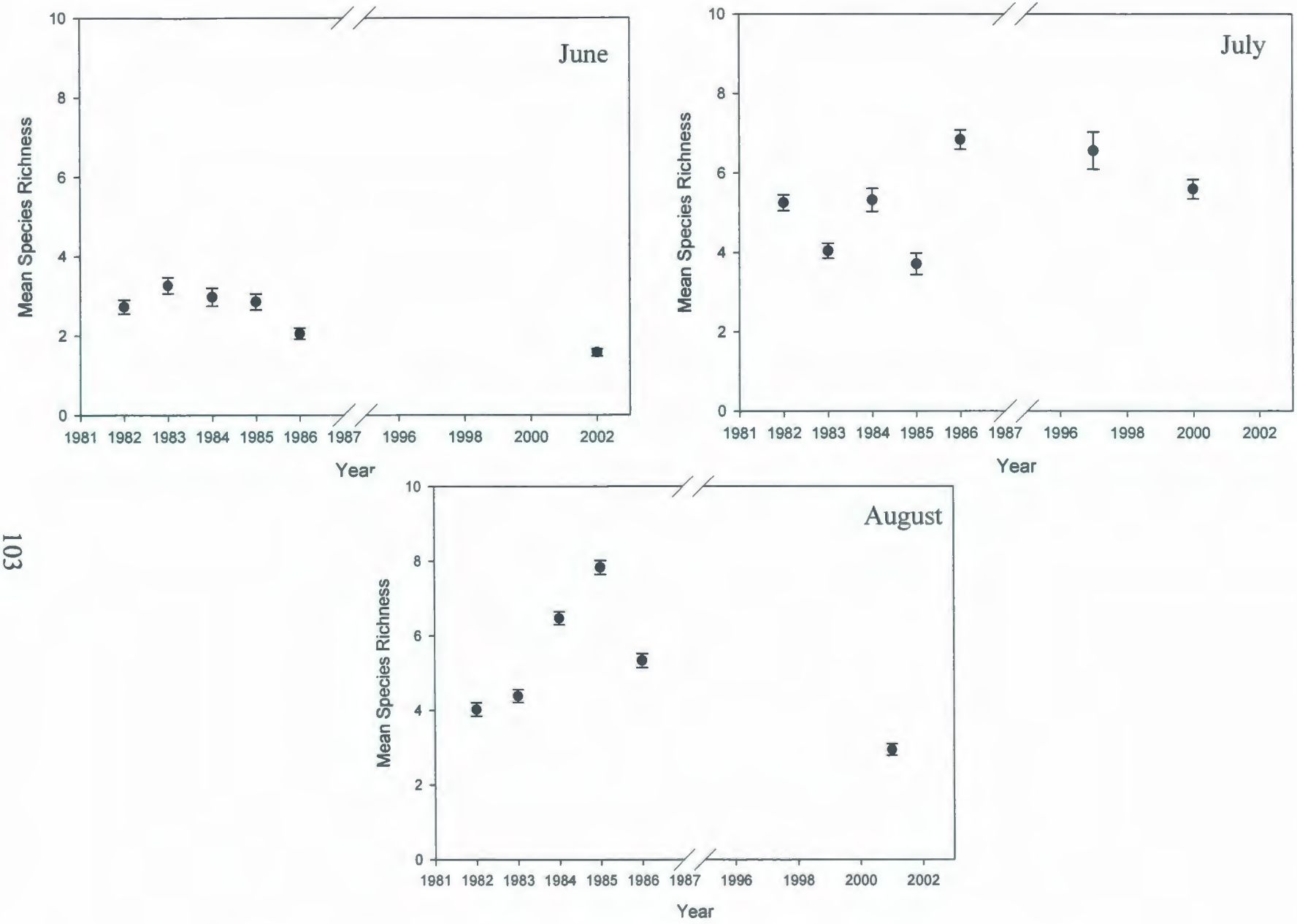

Figure 3-20: Trinity Bay 1982-2002 June-Aug Species Richness. Bars denote standard errors.

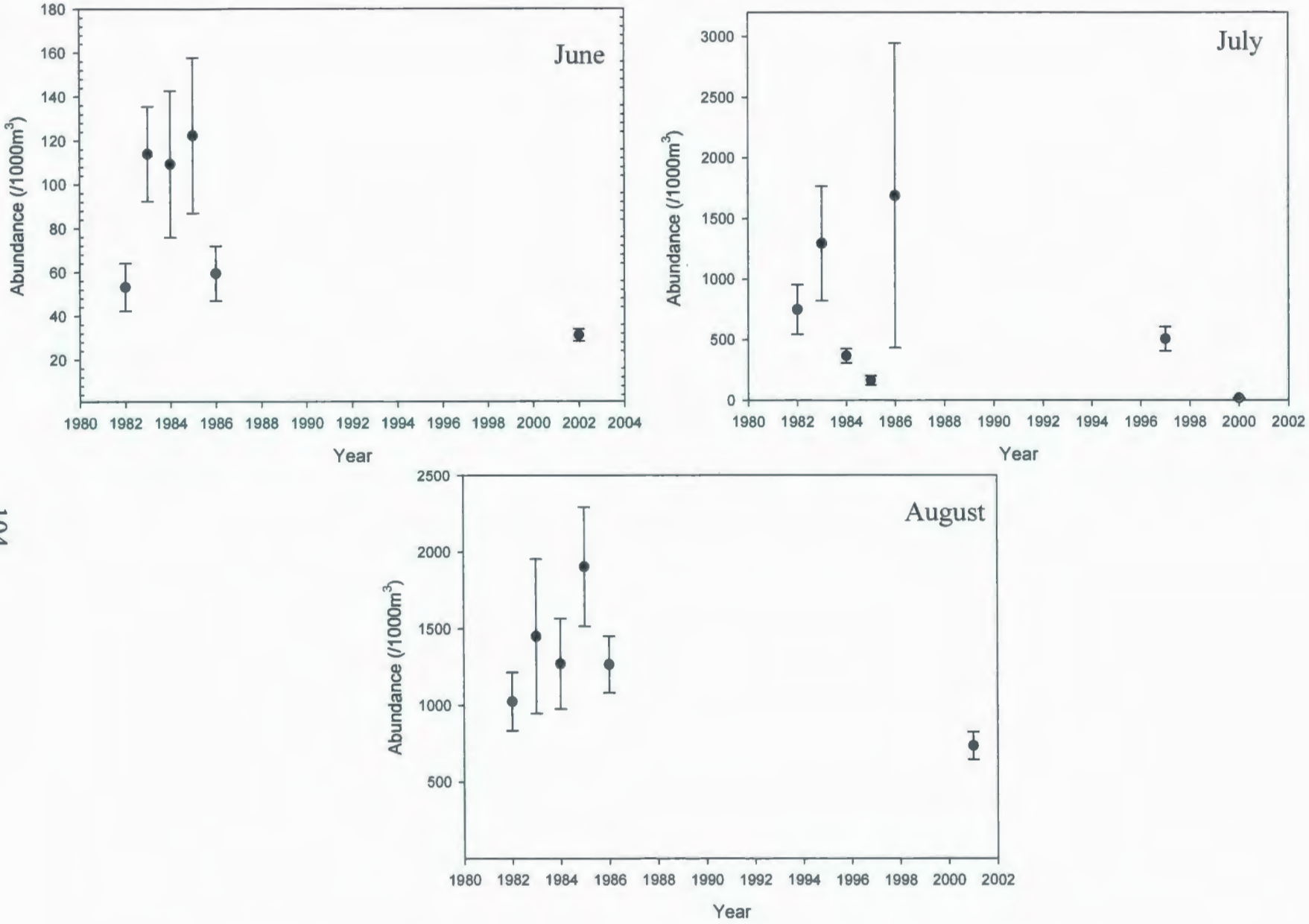

Figure 3-21: Trinity Bay 1982-2002 June-Aug Mean Species Abundance. Bars denote standard errors.

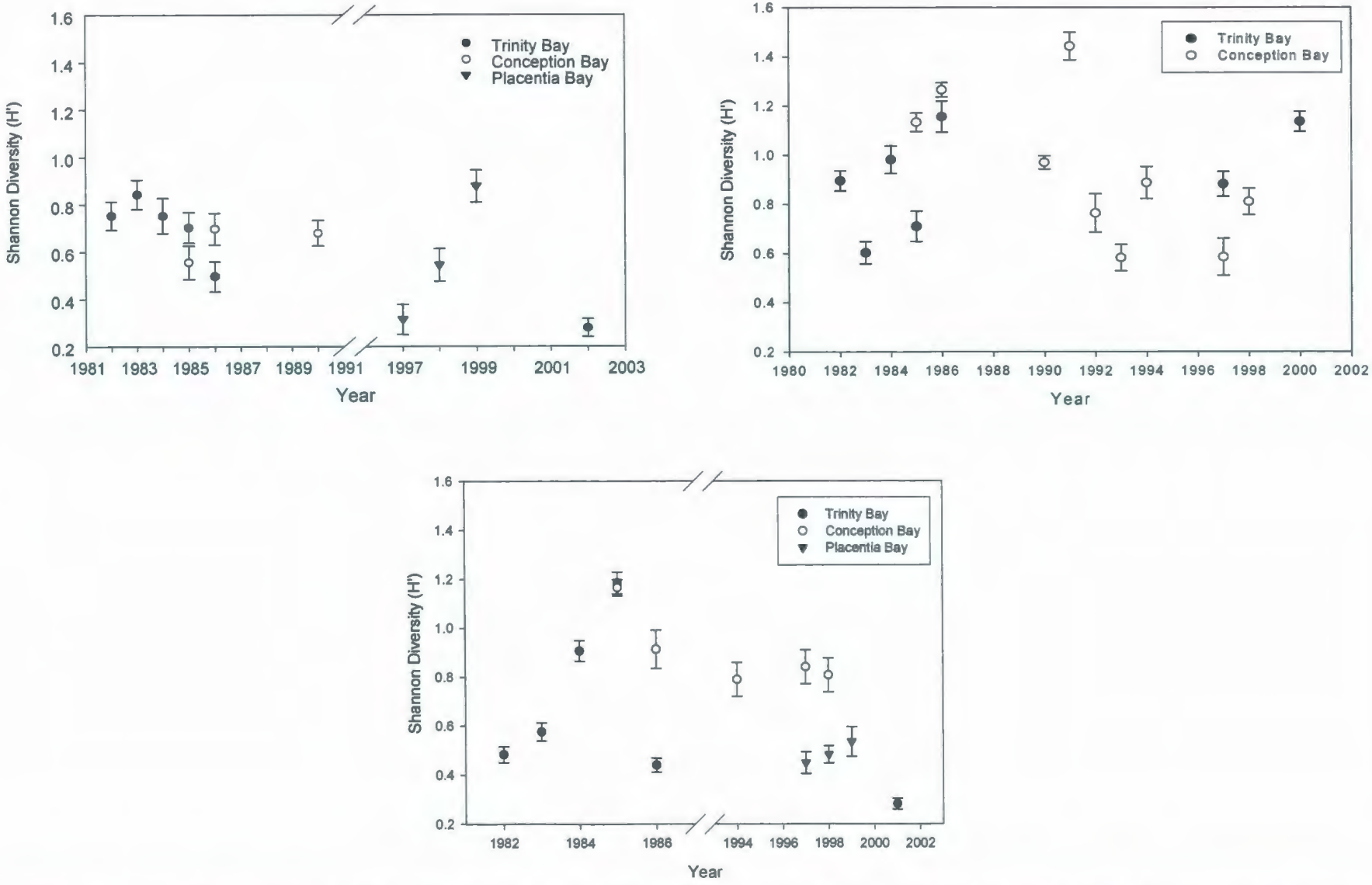

Figure 3-22: Trinity Bay, Conception Bay and Placentia Bay 1982-2002 June-Aug Shannon Weiner Diversity.Bars denote standard errors.

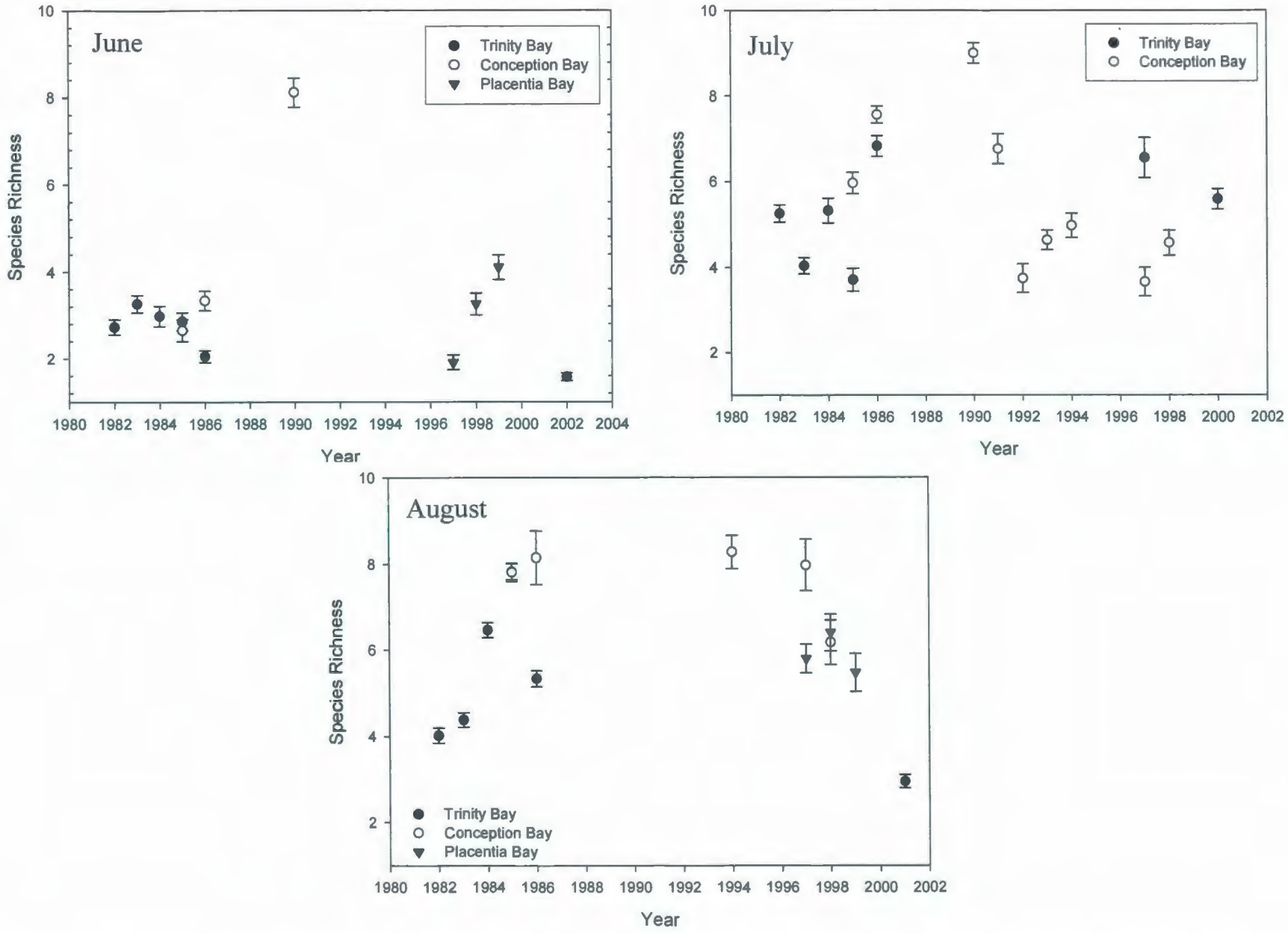

Figure 3-23: Trinity Bay, Conception Bay and Placentia Bay 1982-2002 June-Aug Species Richness. Bars denote standard errors.

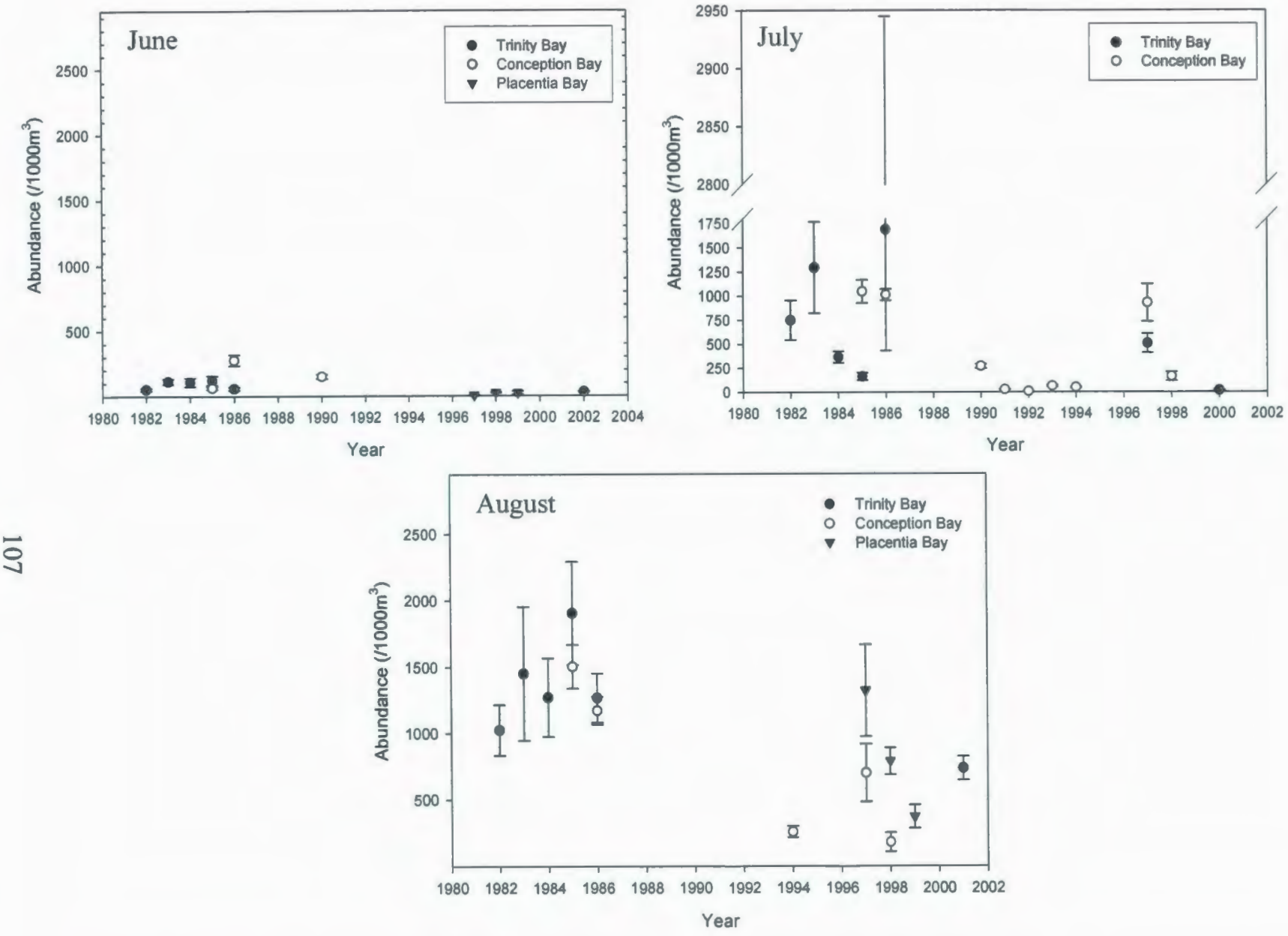

Figure 3-24: Trinity Bay, Conception Bay and Placentia Bay 1982-2002 June-Aug Species Abundance. Bars denote standard errors.

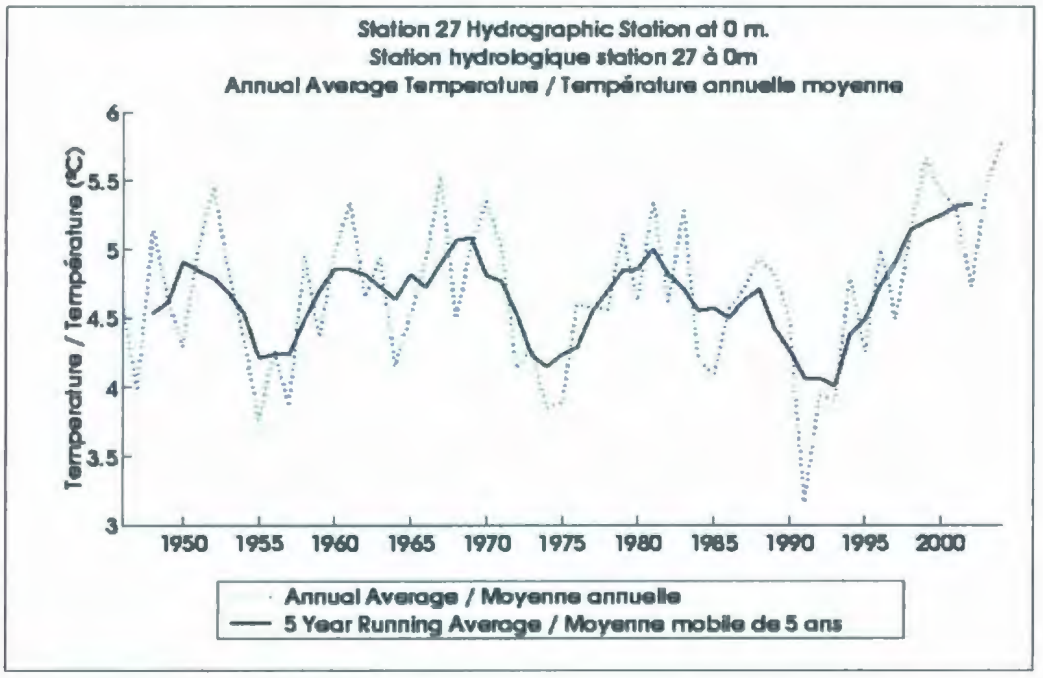

Figure 3-25: Annual average and five year running average of sea surface water temperatures at Station 27 from 1950-2000. Reproduced from Craig and Colbourne (2002).

Table 3-1: Species richness and most abundant species for seasonal larval fish communities in Placentia Bay, 1997-1999 based on species abundance graphs.

Seasonal Grouping	Species Richness	Five Most Abundant Species
Spring (April/May)	29	1) Sandlance (*Ammodytes* sp.) 2) Arctic Shanny (*Stichaeus punctatus)* 3) Shorthorn Sculpin (*Myoxocephalus scorpius*) 4) Radiated Shanny (*Ulvaria subbifurcata)* 5) Snail Fish (*Liparis* sp.)
Transition (June)	13	1) Snail Fish (*Liparis* sp.) 2) Sandlance (*Ammodytes* sp.) 3) Radiated Shanny (*Ulvaria subbifurcata)* 4) Red Fish (*Sebastes* sp.) 5) Atlantic Cod (*Gadus morhua)*
Late Summer (August/September)	20	1) Capelin *(Mallotus villosus)* 2) Cunner (*Tautogolabrus adspersus)* 3) Fourbeard Rockling (*Enchelyopus cimbrius)* 4) Red fish (*Sebastes* sp.) 5) Atlantic Cod (*Gadus morhua)*

Table 3-2: SIMPER analysis results for Trinity Bay June 1982-2002.

	1982-1986	2002				
Species	**Average Abundance (/1000 m^3)**	**Average Abundance (/1000 m^3)**	**Average Dissimilarity**	**Dissimilarity/Standard Deviation**	**% Contribution**	**Cumulative %**
Atlantic Cod *Gadus morhua*	32.08	0.23	23.60	1.96	29.04	29.04
Pollock *Pollachius virens*	9.54	38.87	19.44	1.07	23.92	52.96
Radiated Shanny *Ulvaria subbifurcata*	14.97	2.81	9.58	0.80	11.78	64.74
Atlantic Herring *Clupea harengus*	26.76	1.10	8.07	0.65	9.93	74.67
Rock Gunnel *Pholis gunnellus*	3.21	0.80	5.31	0.58	6.53	81.20
American Plaice *Hippoglossoides platessoides*	1.21	1.86	4.55	0.46	5.59	86.79
Snail Fish *Liparis* sp.	0.04	1.88	3.14	0.39	3.87	90.66

Table 3-3: Trinity Bay post 1992 July abundance data compared with data collected prior to the fisheries closures. Data range extends only until the year 2000.

Commercial	Non-Commercial	Average Abundance Prior to 1992 (larvae/1000m^3)	Average Abundance Post 1992 (larvae/1000m^3)	% Change
Gadus morhua		21.43	1.11	- 94.82
Mallotus villosus		784.60	91.18	- 88.38
Hippoglossoides platessoides		35.08	2.35	- 93.30
	Tautogolabrus adspersus	1.40	29.49	+ 95.25
Pseudopleuronectes americanus		11.41	0.16	- 98.60
Limanda ferruginea		1.37	1.54	+ 12.41
	Liparis spp.	2.34	1.93	- 17.52
Clupea harengus		6.26	34.49	+ 450.96
Glyptocephalus cynoglossus		5.68	0.00	- 100
	Stichaeus punctatus	0.05	0.67	+ 1240
Sebastes spp.		8.51	0.34	- 96.00
	Ulvaria subbifurcata	21.79	16.05	- 26.34
	Cottidae family	0.06	0.25	+ 316.66
	Lumpenus spp.	0.10	0.69	+ 590

Table 3-4: Conception Bay post 1992 July abundance data compared with data collected prior to the fisheries closures. Data range extends only until 1998.

Commercial	Non-Commercial	Average Abundance Prior to 1992 (larvae/1000m^3)	Average Abundance Post 1992 (larvae/1000m^3)	% Decline
Gadus morhua		19.26	0.17	99.11
Mallotus villosus		290.75	114.19	60.72
Hippoglossoides platessoides		44.28	0.63	98.58
	Tautogolabrus adspersus	107.96	32.90	69.52
Pseudopleuronectes americanus		30.76	0.97	96.85
Limanda ferruginea		52.34	2.75	94.74
	Liparis spp.	16.38	0.98	94.02
Clupea harengus		29.43	0.60	97.96
	Liparis atlanticus	5.02	0.30	94.02
Glyptocephalus cynoglossus		47.12	0.00	100
	Stichaeus punctatus	1.17	0.15	87.18
Sebastes spp.		0.42	0.07	83.33
	Liparis gibbus	0.72	0.02	97.22
	Lumpenus spp.	0.38	0.11	71.05

Table 3-5: SIMPER analysis results for Conception Bay August 1985-1998.

	1985-86	1994 &1997-98				
Species	**Average Abundance (/1000 m^3)**	**Average Abundance (/1000 m^3)**	**Average Dissimilarity**	**Dissimilarity/Standard Deviation**	**% Contribution**	**Cumulative %**
Witch Flounder *Glyptocephalus cynoglossus*	134.27	0.83	8.52	1.98	15.89	15.89
Cunner *Tautogolabrus adspersus*	568.71	54.18	8.42	1.66	15.70	31.59
American Plaice *Hippoglossoides platessoides*	3.07	1.14	2.63	1.53	4.90	36.49
Atlantic Cod *Gadus morhua*	20.29	0.99	3.47	1.47	6.97	43.46
Yellowtail Flounder *Limanda ferruginea*	20.19	4.56	3.50	1.46	6.52	49.98
Radiated Shanny *Ulvaria subbifurcata*	37.38	12.34	3.63	1.36	6.77	56.75
Capelin *Mallotus villosus*	700.18	93.97	7.61	1.31	14.18	70.93

IV. Within and Between Bay Variation in Community Composition of Fish Larvae in Coastal Newfoundland

i. Introduction

The last decade has seen a resurgence of interest in marine biodiversity (e.g. Malakoff 2003); in the context of larval fishes this interest stems in part from conservation objectives as well as a desire to understand changes beyond single species and move management towards ecosystem-based decision making (e.g. Botsford et al. 1997). Though appealing in its breadth, multispecies approaches are still evolving. Species diversity is scale dependent (Shackell and Frank, 2000; Shackell and Frank, 2003), however, variations in space and time are difficult to separate and assess independently, complicating the measurement of scale-dependent changes in biodiversity. This is particularly the case in the marine environment where multiple species co-occur in interact in complex ways with each other and with the local environment. Whether species assemblages represent consistent or variable patterns of community structure and species diversity is a subject of some debate (Karakassis et al., 2006). The assumption that data from a given survey can be treated as fixed in time and space, despite some movement of the fish populations during the study period, is common in scientific studies (Warren, 1997), but the dynamic nature of marine ecosystems also makes spatial and temporal comparisons difficult.

Diversity may be assessed at either the alpha, within-community level, or at the beta, among community scale (Whittaker 1972; Loreau, 2000). Within-community and beta measures of diversity are both informative in that within-community diversity provides information about communities from local areas (within a single habitat), whereas

among-community diversity provides information regarding the differentiation of communities along habitat gradients (Whittaker, 1972) within a given geographic region. Three key hypothesis regarding area-dependent relationships of biodiversity are commonly applied in a range of biological systems, including freshwater and island biogeography (Connor and McCoy, 2001), and more recently these same theories have been applied to ocean systems (Frank and Shackell, 2001). (1) Species-area relationships are defined as the observation that the number of biological species found in a region is a function of the area of the region that is sampled. (2) The habitat-diversity hypothesis attributes this relationship to a greater range of habitats in larger regions as a consequence of greater area, resulting in a greater number of species encountered in that region. The species-area hypothesis suggests that area and variation in habitat type are independent, and increased species number is a function of increased abundance of each species in a sample region, and therefore varies as a positive function of that region's area. Specifically, the probability of each species becoming extinct in that area is a negative function of abundance, and consequently area. (3) The third theory is the passive-sampling hypothesis, which states that larger areas are more likely to receive more colonists, and are therefore more likely to contain a more diverse collection of species (Connor and McCoy, 2001).

Regardless of scale, there are numerous complications in attempting to explain spatial patterns of larval fish. Different species of larvae are driven by alternative life history strategies and complex interactions between hydrography and behaviour (Shackell and Frank, 2000; Bradbury et al., 2003). Multiple hypotheses regarding the underlying

processes that drive these patterns have been proposed (Shackell and Frank, 2000; Bradbury and Snelgrove, 2001; Connor and McCoy, 2001; Frank and Shackell, 2001; Bradbury et al., 2003; Shackell and Frank, 2003), however, insufficient data and the large scale of marine ecosystems make it difficult to draw definitive conclusions regarding variability in larval fish biodiversity (Frank and Shackell, 2001).

Adult spawning location and behaviour also contribute to larval diversity. Mueter and Norcross (2002) showed that depth is important in structuring adult groundfish communities, with pronounced peaks in species richness, diversity and biomass at intermediate depths (150 m – 300 m). They went on to propose that the observed peaks in diversity and abundance at intermediate depths were a consequence of favourable feeding conditions created by enhanced benthic productivity associated with shelf break fronts, seasonal upwelling, strong alongshore currents, and tidal mixing (Parsons, 1986 in Mueter and Norcross, 2002). Similarly, theories such as the match-mismatch hypothesis (Cushing, 1966; Cushing, 1995) relate larval fish abundance and adult spawning strategies to areas with peak prey availability (Shackell and Frank, 2000). Bradbury et al. (2000, 2003) discuss the ability of larger larvae to move actively toward areas of greater food availability and to avoid advective processes that may result in decreased larval retention (larvae remaining near their point of origin whether by active or passive mechanisms (Warner and Cowan, 2002)), in inshore waters where larval survival is believed to be greatest (see also Snelgrove et al., 2008).

Water temperature is an important contributor to larval retention, development and survival (Bradbury et al., 2001). Within Newfoundland coastal waters, seasonal ice cover and currents affect bays on the north and south coasts of the island differently. The inshore branch of the cold Labrador Current passes along the shores of both Trinity and Conception Bays (Sheng and Thompson, 1996) on the north coast. On the south coast, Placentia Bay is influenced by water currents branching from the Labrador Current (Sheng and Thompson, 1996), but also by the warmer Gulf Stream waters that flow south of Newfoundland and influence both Placentia and Fortune Bays (Hay and deYoung, 1989). One result of this circulation pattern is increased sea ice in Trinity and Conception Bays compared to Placentia and Fortune Bays.

The observation of differences in the dominance structure of the larval fish communities (Chapter 3) between Trinity and Conception Bays and Placentia Bay suggests that differences in assemblages may result from differences in water temperatures (via currents) or the different water mass sources that influence the bays. In Chapter 3 abundance of colder water species in Trinity and Conception Bays were higher than those in Placentia Bay.. These findings raise the question of whether temporal changes have occurred in species diversity or dominance of larval fish over a large spatial scale (100's of km) during the last two decades, a period when major changes have occurred in commercial fisheries. Specifically, this study addresses whether changes in ichthyoplankton are analogous among the bays surrounding Newfoundland's Avalon Peninsula or whether changes in the larval fish community occur primarily at a within-

bay spatial scale. In other words is the spatial variation within the bays greater or less than spatial variation among the bays?

ii. Methods

Data Collection

Data used in this study were collected during the summers (June-August) of 1982, 1985/86 and 1998; these data represent instances where near-simultaneous collections were carried out in more than one embayment. The data were collected in one of four Newfoundland embayments; Trinity Bay, Conception Bay, Fortune Bay or Placentia Bay (Figure 3-1). Trinity Bay is located on the northeast coast of Newfoundland and measures approximately 100 km long by 30 km wide, with a maximum depth of 630 m in a deep trench located near the centre of the bay (Pepin et. al., 2005). A sill at the mouth of the bay has a maximum depth of 240 m. Wind forcing has a major effect on the stratification and circulation of the bay (Yao, 1986; Davidson et. al., 2001). During the time of sample collection (summer months), southwesterly longshore winds are predominant, creating local upwelling areas. Conception Bay is approximately 50 km long by 25 km wide with a maximum depth of roughly 300 m. A sill at the mouth of the bay has a maximum depth of 150 m. Like Trinity Bay, Conception Bay is susceptible to wind forcing but on shorter time scales (Pepin et al., 1995). Placentia Bay is located on the southeast coast of the Avalon Peninsula and measures approximately 130 km long by 100 km at its widest point near the mouth of the bay (Bradbury et al., 2000). Depth is greater than 300 meters in some areas, and currents generally flow into the bay along the eastern shore and out along the western shore (Bradbury et al., 2000). Unlike the bays on the north coast, pack ice is

rare and spring bloom dynamics are unrelated to ice break-up. Fortune Bay is an unusually wide fjord bordered by the Burin Peninsula to the east and by Hermitage Channel to the west. The bay is located on the south coast of Newfoundland, directly west of Placentia Bay. Fortune Bay is 128 km long and 22 km wide and has a maximum depth of 420 m in the main basin. There are three silled entrances to the fjord with bottom depths of approximately 125 m (deYoung and Hay, 1987). Mean wind speeds for Fortune Bay during the summer months (??) are ~ 2.7 m s^{-1} directed essentially parallel with the bay axis (White and Hay, 1994). Both the NE and SE components of the wind showed variability at long periods of l0-15 days, as well as a fairly strong oscillations with a period of about 3 days.

Data from Trinity Bay were collected using a 61-cm bongo net (side unspecified) fitted with 333 μm mesh nitex. Data from Conception Bay were collected using either a 50 cm ring net fitted with 165 μm mesh or a 4 m^2 Tucker trawl consisting of three sections fitted with 1000-, 505-, and 333- μm mesh. Each bongo net or Tucker trawl sample consisted of an oblique tow of approximately 15 min at a tow speed of approximately 2-3 kn. The nets were lowered to a depth approximately 5-10 m from the sea floor or to a maximum depth of 200 m. Each ring net sample consisted of a single horizontal tow of approximately 15 min at 7 m with a tow speed of roughly 2-3 kn. Volume filtered was estimated using a General Oceanics flowmeter positioned at the mouth of each net. Data from Placentia Bay were collected along a grid of 45 stations (Figure 3-2) that were sampled between 07:00 and 19:00 h with a 4 m^2 Tucker trawl fitted with 1000-, 505-, and 333- μm mesh

(Bradbury et al., 2000). The Tucker trawl was deployed using oblique tows to a depth of 40 m at a tow speed of approximately 2 kn (Bradbury et al., 2000).

Data Analysis

The analysis presented here extends comparisons beyond the seasonal variation and long-term changes in pattern described in Chapter 3, and are directed towards documenting spatial and/or environmental differences among bays and coasts.

Paired comparisons between Trinity and Fortune Bays, Trinity and Conception Bays, and Conception and Placentia Bays were used for spatial analysis because these data sets were collected within either the same cruise or within the same month and year. Data were analyzed using PRIMER, except where otherwise noted. Comparisons were made by first generating a species by sample matrix using standardized concentrations (individuals·1000m^{-3}) from each data set. The data was then fourth root transformed (Field et al., 1982; Clarke and Warwick, 2001) prior to generating a Bray-Curtis similarity matrix. Fourth root transformation reduces the relative importance of the most abundant species; similarities subsequently depend not only on abundant species, but also on less common ("mid-range") and rare species (Clarke and Warwick, 2001). Bray-Curtis is biased toward dominant species but transformations counteract this bias. A common characteristic of marine survey data is that many of the species are absent from a large number of the samples. Typically greater than half the data matrix entries are zeros and transformation of the data has no effect on zero values (Field et al., 1982). The Bray-Curtis similarity measure was selected for use because it is unaffected by joint absences

(Clarke and Warwick, 2001), and species that are absent from a given comparison of no effect on their similarity. Similarity matrices were then assessed using group-average clustering methods and multi-dimensional scaling plots to determine whether samples collected closer to one another in space are more similar than those collected from greater distances.

Similarity percentages (SIMPER) were used to determine which species were most responsible for the Bray–Curtis dissimilarities between-bays.. SIMPER analysis was completed using the software package Primer (Plymouth Routines In Multivariate Ecological Research). SIMPER estimates the contribution of individual taxa to similarity among treatments and is used to determine the extent to which individual species were responsible for the patterns detected by group average cluster analysis or stations grouped by sampling region, which in this case is individual bays (Caldeira, 2002). These analyses make it possible to compare species composition between bays at selected points in time to determine which species drive those differences. Some time-independent variation between the bays is expected given their geographic locations and physical differences, such as the greater average depth of Trinity Bay compared to Conception Bay.

The final analysis compared Shannon-Wiener diversity, species richness, and abundance between bays that were sampled during the same cruise or/month. For each bay, the variance around the mean for Shannon-Wiener diversity, species richness and abundance were calculated and compared for heteroscedasticity using Hartley's F_{max} – test (Sokal and Rohlf, 2000).

$$F_{max} = s^2_{max} / s^2_{min} \qquad (3)$$

Shannon-Wiener diversity index (H) was computed for each sample using the formula:

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where H is the diversity in s species, s is the number of species present in the sample, p_i is the proportion of species i in the sample (n_i/n), and $\sum p_i = 1$. An estimate of H is therefore,

$$H = -\sum_{i=1}^{s} (n_i / n) \ln(n_i / n) \qquad (2)$$

given a random sample of n (total number of individuals in the sample from all species) observations from data in the s species i (1, 2, . . ., s) with probabilities p_i (1, 2, . . ., s), where h and H fall between zero and ln s (Hutcheson, 1970).

The means were compared using either t-tests for two independent means on non-transformed data or, in instances where heterogeneity of variance was found, the bays were compared using Mann-Whitney U-tests for independent means. Between bay comparisons that showed no significant difference at p = 0.05 were concluded to have comparable diversity, species richness, or abundance.

iii. Results

Multidimensional scaling plots and group average cluster analysis revealed the presence of between-bay as well as within-bay spatial variation in larval fish assemblages that varied as a function of time period. Comparisons from August 1998 between Placentia Bay and Conception Bay, which are separated by the Avalon Peninsula, showed both within bay and between bay differences in species composition (Figs 4-1, 4-2). Differences were observed between the head and mouths of both bays (Fig. 4-2). SIMPER analysis that explored differences in community composition of larvae between the heads and mouths of the bays showed that the mouth of Conception Bay had the greatest dissimilarity from other areas within Conception and Placentia Bays. The mouth of Conception Bay was more similar to the head of Conception Bay than to the mouth of Placentia Bay (Tables 4-1, 4-2, 4-3). Although the MDS plots show no clear between-bay spatial differences, the two separate clusters of Conception Bay stations likely reflect differences in community composition between the head and mouth of the bay. Conception and Placentia Bays, though indistinct in MDS plots, nonetheless differed from one another in some aspects of community composition (Table 4-1). SIMPER analysis shows that the primary difference between the two bays was higher abundances of capelin and cunner in Placentia Bay. These two species account for 41.62% of the dissimilarity between Conception and Placentia Bays. Atlantic cod was also more abundant in Placentia Bay, and accounted for 8.25% of the between-bay dissimilarity. Together these three species account for nearly half of the dissimilarity. Mann-Whitney U tests and t-tests comparing Shannon-Wiener diversity, richness and abundances between the two bays showed significantly higher Shannon-Wiener Diversity ($p = 0.001$,

n = 81) in Conception Bay, no difference in species richness ($p = 0.134$, $n = 81$), and significantly higher abundance ($p = 0.001$, $n = 81$) in Placentia Bay (Table 4-4).

Multidimensional scaling and cluster analysis of Trinity and Fortune Bay data from July 1982 showed clear between-bay differences (Figure 4-3) with stations from the two bays forming separate and distinct clusters. SIMPER analysis showed a 70.21 % average dissimilarity in species composition between the two bays with American plaice, Atlantic cod and capelin contributing 49.35% to overall dissimilarity (Table 4-5). Mann-Whitney U tests and t-tests comparing Shannon-Wiener diversity, richness and abundances between the two bays showed significantly higher richness ($p < 0.001$, $n = 108$) and significantly higher abundance ($p < 0.001$, $n = 108$) in Trinity Bay, but no difference in Shannon-Wiener diversity ($p = 0.210$, $n = 108$) (Table 4-6).

Multidimensional scaling and cluster analysis of Trinity and Conception Bay data collected from June-August 1985 and 1986 showed differences in species composition between the two bays in both years (Figs. 4-4, 4-5). SIMPER analysis of the two years showed 71.72 % average dissimilarity in species composition between the two bays in 1985 and 64.85 % average dissimilarity in species composition between the two bays in 1986 (Tables 4-7, 4-8). Mann-Whitney U tests and t-tests comparing Shannon-Wiener diversity, richness and abundances between the two bays showed significantly greater richness in Conception Bay than Trinity Bay during July 1985 and significantly greater richness in Trinity Bay in August of 1985 and in Conception Bay in August 1986.

Significantly higher abundances were also observed in Conception Bay during July 1985 and June 1986. No difference was found for Shannon-Wiener diversity (See Chapter 2).

iv. Discussion

Based on MDS results presented here, Trinity and Conception Bays appear to be more similar to each other in species composition than to Placentia and Fortune Bays. Additionally, bays located further north were found to be more diverse than southern bays. Although limited by their discrete timing, these comparisons show that during the early 1980's the northern bays had greater larval abundance than the southern bays. In contrast, during the late 1990's larval abundance was greater in the southern bays, a trend also noted by Rose et al. (2000) for adult fish assemblages . There were also between-bay differences in larval fish assemblages sampled during the same time period. As shown in the Trinity and Conception Bay comparison (Figure 4-4, Table 4-7), despite substantial within-bay variability, there were large-scale between-bay patterns in assemblages and community parameters (see Chapter 3). Many of the abundant species in Trinity, Conception and Placentia Bays were common to all bays; however, there were differences in dominance structure. Fortune Bay was less diverse than Trinity Bay (Table 4-5, Table 4-6), partly as a result of the absence of several colder water species such as arctic shanny; which may reflect the influence of the Gulf Steam and warmer waters in Fortune Bay. Further analysis is required to determine the causes of these differences.

The Placentia and Conception Bay comparison also suggests that there is substantial within-bay variability in species composition (Figure 4-2). In both Conception and Placentia Bays, capelin (*M. villosus*) and cunner (*T. adspersus*) contributed most strongly to within-bay differences in species composition (Table 4-3). In Conception Bay these species were most abundant near the mouth of the bay whereas the opposite was true for Placentia Bay. This pattern could reflect differences in spawning strategies by adults or the interaction of mean currents and temperature.

As discussed by Bradbury et al. (2001) there are strong indications that adult spawners make use of recurring spawning locations, resulting in distinct larval distributions for Atlantic cod. These distributions have been hypothesised to be the consequence of spawning strategies that place eggs and larvae in areas with optimal hydrographic features that help to enhance larval retention (Laprise and Pepin, 1995). Larval retention within the bays is believed to increase larval survival because offshore transport may reduce availability of suitable habitat and increase predation rates (Bradbury et al., 2001). Temperature can play a significant role in larval retention as a result of its effect on developmental rate (Pepin et al., 1997; Bradbury et al., 2000; Bradbury et al., 2001). Temperature directly affects developmental rate of eggs and larvae because eggs and larvae develop at a slower rate in cooler temperatures. Bradbury et al. (2001) argued that large numbers of cod eggs spawned in Placentia Bay during the spring months produced fewer larvae than did a smaller number of eggs spawned in late summer months because slower development in spring meant that eggs required longer periods to hatch and therefore experienced higher predation and advective loss. In late summer, eggs hatched

quickly and larvae were soon large enough to contribute to pattern through active movement (Bradbury et al. 2001). Therefore, despite hydrographic linkage between spawning and nursery grounds, recruitment success in relation to these features may depend on temperature, and at a regional scale, seasonality or widespread temperature anomalies can result in correlated shifts of larval abundance and diversity.

Laprise and Pepin (1995) describe two larval habitat categories: biologically ideal habitat characterized by abundant food with few predators, and physico-chemically ideal habitat characterized by temperature/salinity properties or high larval retention/transport to nursery grounds. In contrast to the present findings, Laprise and Pepin (1995) found that the highest abundances of all larval species were usually found at the head of Conception Bay in association with the warmest waters. Bradbury et al. (2000) reported a strong seasonal relationship between the highest concentrations of late stage eggs and larval Atlantic cod near the western mouth of Placentia Bay and the warmest summer water temperatures. Data from Conception Bay presented here showed that with the exception of radiated shanny and fourbeard rockling, larvae were in greater abundance at the mouth of the bay (Table 4-3). The differences in within-bay larval patterns found between the present study and that of Laprise and Pepin (1995) could be affected by the time of sampling. Based on previous analysis, when Laprise and Pepin sampled in 1991, this was an anomalous year during which larval fish composition was regionally quite different from that typically observed during other years (see Chapter 3). Therefore, it is possible that the distribution of larvae observed here (August 1998) might be more representative of "typical" larval distributions. Additionally, the influence of factors such as

temperature, mesozooplankton distribution and abundance, as well as the effect of increased invertebrate biomass and distribution shifts after the groundfish collapse (Drinkwater and Mountain, 1997; Rose et al., 2000), which have not been explored here, merit further investigation for this time period.

Data collected within the same month minimizes any seasonal influence, which Methven et al. (2001) concluded had the greatest effect in structuring inshore, estuarine juvenile fish assemblages in Trinity Bay. Therefore, within-bay spatial patterns in larval diversity shown here are believed to be driven by processes other than temporal variation. There is support for habitat-diversity explanations if Fortune Bay is included in the analysis and if specific regions within the bays are examined. Trinity and Conception Bays do not differ consistently in diversity (Table 2-1), or environmental conditions (i.e. these bays experience similar ice coverage, wind forcing and temperature fluctuations). Shallow regions within the bays may provide habitat dissimilar to deeper areas. Species dominance within the bays is primarily responsible for the observed differences because the majority of species that contribute to between-bay differences differ only in relative abundance and there are no apparent differences in species richness (Tables 4-8, 4-9). It is important to note that this result may be related to water mass effects caused by the close proximity of Fortune Bay to the northern branch of the Gulf Stream, but the data presented here represent just one month of a single year. Similarly caution must be exercised in the interpretation of Placentia and Conception Bay comparison (Table 4-1).

The species-area hypothesis is not supported by these data; despite differences in sampling area (Fortune Bay greater than Trinity Bay and Trinity Bay greater than Conception Bay) species richness does not appear to differ between bays. Similar numbers and composition of species were observed throughout all four bays sampled in this study. It may be difficult to apply area-based theories to ichthyoplankton, particularly in embayments where habitat complexity may not correlate with total area. As described by Laprise and Pepin (1995), many larval fish habitats are characterized by distinct environmental characteristics. In this way, it is possible to have numerous pockets of ideal conditions so that even studies that range over hundreds of kilometres may not be large enough to elucidate scale-dependent patterns.

In conclusion, truly concurrent collections within each of the individual bays would be extremely useful in making diversity comparisons. Although not considered here, regional geography may determine diversity in this region, in that Fortune and Placentia Bays may not support the same numbers of cold-water species as the northern bays, which are more strongly affected by the Labrador Current. Because the northern bays are more strongly affected by this colder water mass it is possible that they provide ideal habitat for a broader range of both temperate and sub-arctic species.

Further investigation into smaller-scale factors that may affect diversity, in addition to data collected more closely in time, are needed to make more conclusive arguments on scale dependence of larval fish diversity in this region. Greater understanding of the within-bay spatial patterns may allow more accurate predictions on spawning strategies

and nursery grounds of individual species. Local patterns provide a starting base for studies on large-scale interannual and seasonal variation, as well as changes related to overfishing.

v. Literature Cited

Botsford, L. W., J. C. Castilla, and C. H. Peterson. (1997) The management of fisheries and marine ecosystems. Science 277:509–515.

Bradbury, I. R., P.V.R. Snelgrove, and S. Fraser (2000) Transport and development of eggs and larvae of Atlantic cod, *Gadus morhua*, in relation to spawning time and location in coastal Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences. 57: 1761-1772.

Bradbury, I.R. and P.V.R. Snelgrove (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. Canadian Journal of Fisheries and Aquatic Sciences. 58: 811-823.

Bradbury, I. R., P.V.R. Snelgrove and S. Fraser (2001) The influence of temperature on advective loss of Atlantic cod (*Gadus morhua*) eggs from the inshore environment. Fisheries Oceanography. 10: 342-352.

Bradbury, I. B., P.V.R. Snelgrove and P. Pepin (2003) Passive and active behavioural contributions to patchiness and spatial pattern during the early life history of marine fishes. Marine Ecology Progress Series. 257: 233-245.

Caldeira, R.M.A. (2002) Multidisciplinary oceanographic studies of a small island in the Southern California Bight. PhD Thesis. University of California. Los Angeles.

Clarke, K.R. & R.M. Warwick (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd Ed. PRIMER-E: Plymouth.

Cushing, D. H. (1966). Biological and hydrographic changes in British seas durng the last thriy years. Biological. Reviews. 41: 221–258.

Cushing DH (1995) Population production and regulation in the sea, a fisheries perspective. Cambridge University Press, Cambridge.

Connor, E. F. and E. D. McCoy (2001) Species-area relationships. *In* Encyclopaedia of biodiversity. v. 5. Academic Press, San Diego, California. pp. 397-411.

Davidson F.J.M., R. Greatbatch and B. deYoung. (2001) Asymmetry in the response of a stratified coastal embayment to wind forcing. Journal of Geophysical Research.106: 7001-7017.

De Young, B. and A. E. Hay (1987) Density Current Flow into Fortune Bay, Newfoundland. Journal of Physical Oceanography. 17: 1066-1070.

Drinkwater, K.F. and D.G. Mountain (1997) Climate and oceanography. *In* Northwest Atlantic groundfish: perspectives on a fishery collapse. American Fisheries Society, Bethesda, Maryland. pp. 3-25.

Field, J.G., K.R. Clarke & R.M. Warwick (1982) A practical method for analyzing multispecies distribution patterns. Marine Ecology Progress Series 8:37-52.

Frank, K.T. and N.L. Shackell (2001) Area-dependent patterns of finfish diversity in a large marine ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 58: 703-1707.

Hay, A. E. and B. deYoung (1989) An oceanographic flip-flop-Deep water exchange in Fortune Bay, Newfoundland. Journal of Geophysical Research – Oceans. 94(C1):843-853.

Hutcheson, K. (1970) A test for comparing diversities based on the Shannon formula. Theoretical Biology 29: 151-154.

Karakassis, I., A. Machias, P. Pitta, K. N. Papadopoulou, C. J. Smith, E. T. Apostolaki, M. Giannoulaki, D. Koutsoubas and S. Somarakis (2006) Cross-community congruence of patterns in a marine ecosystem: Do the parts reflect the whole? Marine Ecology Progress Series 310: 47-54.

Laprise, R. and P. Pepin (1995) Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. Marine Ecology Progress Series. 122: 73-92.

Loreau, M. (2000) Are communities saturated? On the relationship between α, β and γ diversity. Ecology Letters 3: 73-76.

Malacoff, D. (2003) Scientists Counting on Census to Reveal Marine Biodiversity. Science. 302: 773.

Methven, D. A., R. L. Haedrich and G.A. Rose (2001) The fish assemblage of a Newfoundland estuary: Diel, monthly and annual variation. Estuarine, Coastal and Shelf Science. 52: 669-687.

Mueter, F. J. and B.L. Norcross (2002) Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. Fishery Bulletin. 100: 559-581.

Ouellet, M., B. Petrie and J. Chassé (2003) Temporal and spatial scales of sea-surface temperature variability in Canadian Atlantic waters. Canadian Technical Report Hydrography and Ocean Sciences. 999: v + 30pp.

Parsons, T. R. (1986) Ecological relations. *In* The Gulf of Alaska: physical environment and biological resources (D. W. Hood and S. T. Zimmerman, eds), pp. 561-570. Minerals Management Serviec, Springfield, Virginia.

Pepin, P., D. C. Orr and J.T. Anderson (1997) Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences. 54 (Suppl.1): 2-10.

Pepin, P., P.V.R. Snelgrove and K. P. Carter (2005) Accuracy and precision of the continuous underway fish egg sampler (CUFES) and bongo nets: a comparison of three species of temperate fish. Fisheries Oceanography 14: 432-447.

Rose, G.A., B. deYoung, D.W. Kulka, S.V. Goddard and G.L. Fletcher (2000) Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Can. J. Fish. Aquat. Sci. 57:644-663.

Shackell, N. L. and K. T. Frank (2000) Larval fish diversity on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 57: 1747-1760.

Shackell, N. L. and K. T. Frank (2003) Marine fish diversity on the Scotian Shelf, Canada. Aquatic Conservation: Marine and Freshwater Ecosystems. (in press). (www.interscience.wiley.com) DOI: 10.1002/aqc.554.

Sheng, J. and K.R. Thompson (1996) Summer Surface Circulation on the Newfoundland Shelf and Grand Banks: The Roles of Local Density Gradients and Remote Forcing. Atmosphere-Ocean. 34 (2): 257-284.

Snelgrove, P.V.R., I.R. Bradbury and S. Fraser (2008) Temporal variation in fish egg and larval production by pelagic and demersal spawners in a large Newfoundland coastal embayment. Canadian Journal of Fisheries and Aquatic Sciences. 65: 159-175.

Sokal, R.R. and F.J. Rohlf (2000) Biometry. 3rd ed. W.H. Freeman and Company, New York.

Warner, R.R. and R.K.Cowen (2002) Local retention of production in marine populations: evidence, mechanisms and consequences. Bulletin of Marine Science 70(1) Suppl.: 245-249.

Warren, W.G. (1997) Changes in the within-survey spatio-temporal structure of the northern cod (*Gadus morhua*) population, 1985-1992. Canadian Journal of Fisheries and Aquatic Sciences. 54 (Suppl. 1): 139-148.

White, M. and A.E. Hay (1994) Dense overflow into a large silled embayment: Tidal modulation, fronts and basin modes. Journal of Marine Research 52: 459-487.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. Taxon 2/3: 213-251.

Yao, T. (1986) The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmosphere-Ocean. 24: 235-252.

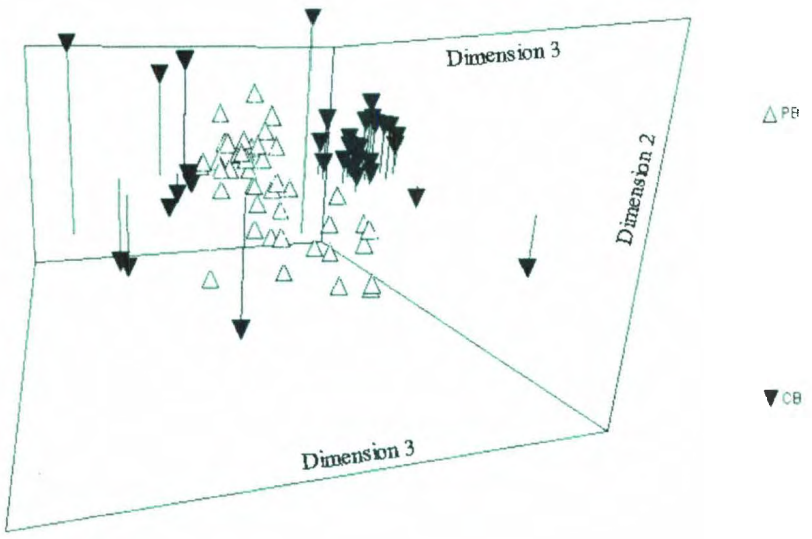

Figure 4-1: Multidimensional Scaling plot of Placentia Bay and Conception Bay data collected during August 1998. Vertical lines represent distance from central z-axis providing reference for data point placement within 3 dimensional space.

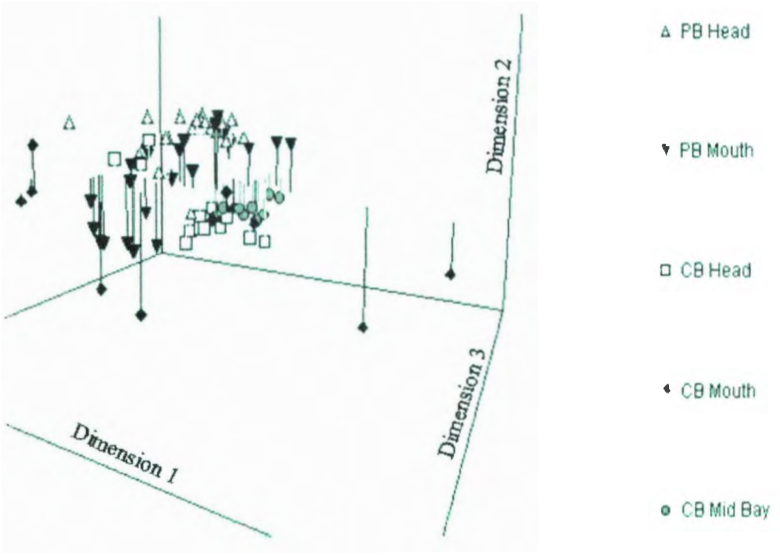

Figure 4-2: Multidimensional Scaling plot of Placentia Bay and Conception Bay data showing regional separations within the bays. Data was collected during August 1998. Vertical lines represent distance from central z-axis providing reference for data point placement within 3 dimensional space.

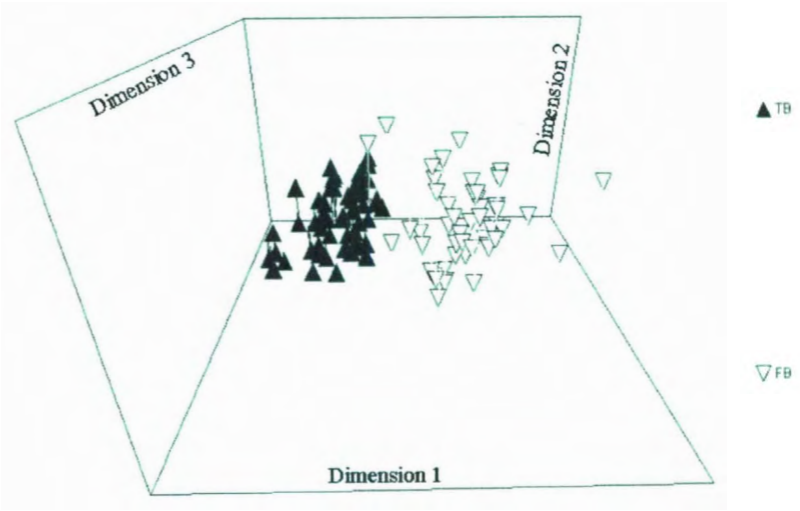

Figure 4-3: Multidirnensional Scaling plot of Trinity Bay and Fortune Bay Data collected during July 1982. Vertical lines represent distance from central z-axis providing reference for data point placement within 3 dimensional space.

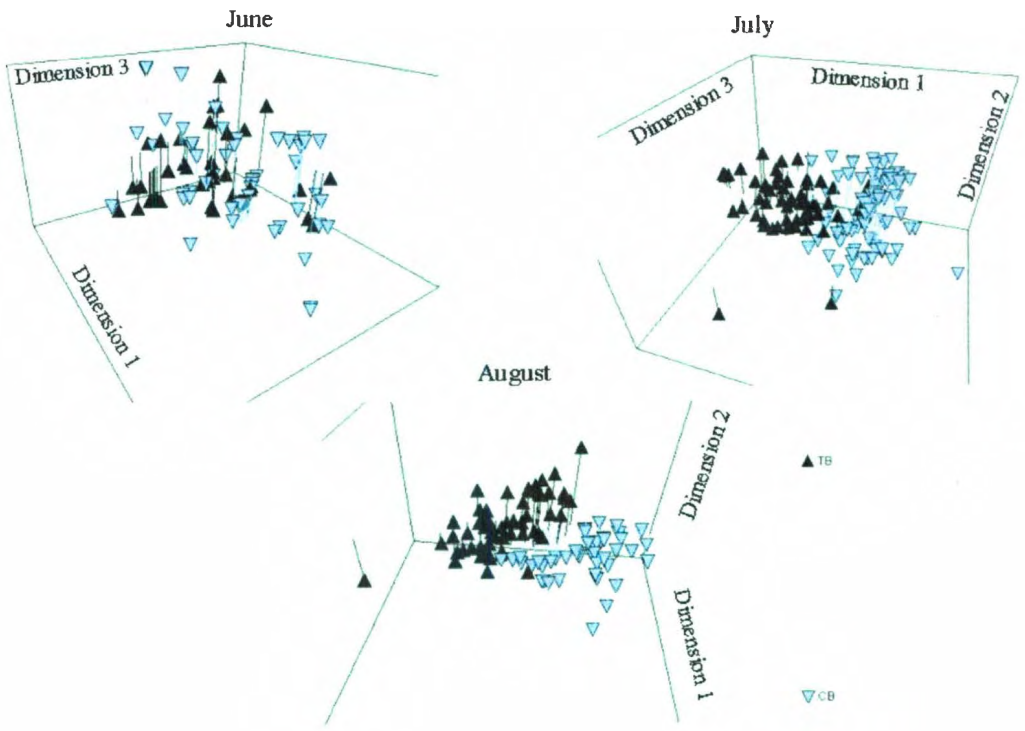

Figure 4-4: Multidimensional Scaling plots of Trinity Bay and Conception Bay data collected during June-Aug 1985.

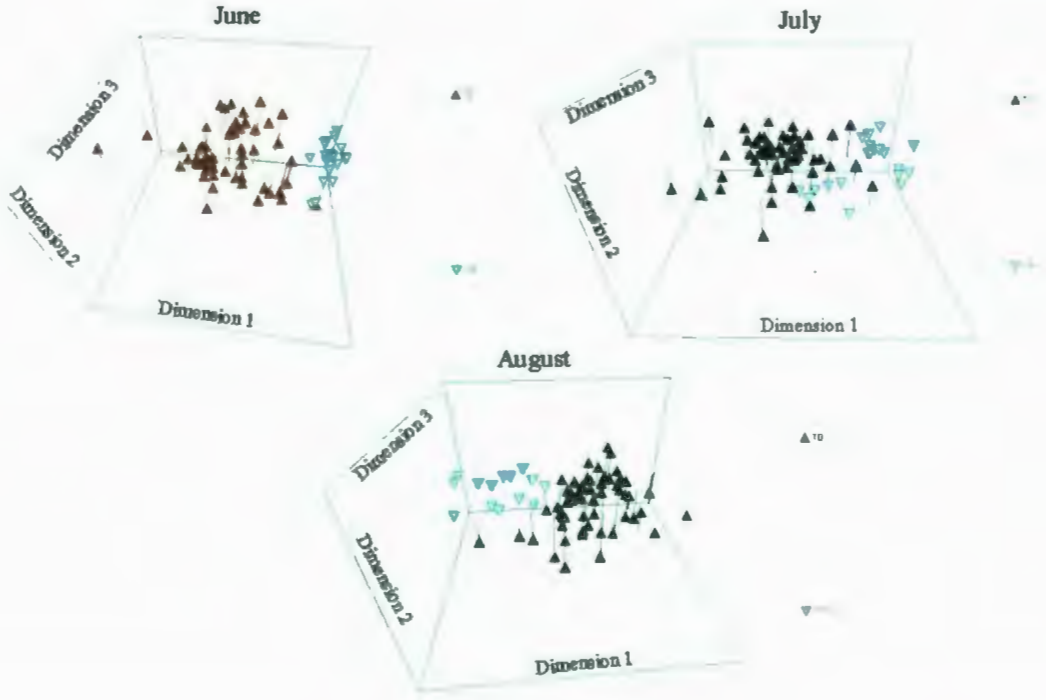

Figure 4-5: Multidimensional Scaling plots of Trinity Bay and Conception Bay data collected during June-Aug 1986.

Table 4-1: SIMPER analysis results for Placentia Bay vs Conception Bay August 1998.

Average Dissimilarity = 53.57	**PB**	**CB**				
Species	**Average Abundance (/1000 m³)**	**Average Abundance (/1000 m³)**	**Average Dissimilarity**	**Dissimilarity/Standard Deviation**	**% Contribution**	**Cumulative %**
Capelin *Mallotis Villosus*	444.21	186.51	11.70	1.26	21.85	21.85
Cunner *Tautogolabrus adspersus*	330.47	103.55	10.59	1.38	19.77	41.62
Atlantic Cod *Gadus morhua*	7.73	0.30	4.42	1.35	8.25	49.88
Yellowtail Flounder *Limanda ferruginea*	0.25	3.66	4.08	0.85	7.61	57.49
Radiated Shanny *Ulvaria subbifurcata*	0.39	2.07	3.86	1.01	7.21	64.70
Snail Fish Sp. *Liparis sp.*	0.38	2.45	3.69	1.01	6.89	71.59
Four Beard Rockling *Enchelyopus cimbrius*	1.16	0.30	3.35	1.35	6.26	77.85
American Plaice *Hippoglossoides platessoides*	0.61	0.40	2.59	1.04	4.84	82.69
Red Fish *Sebastes sp.*	1.12	0.02	2.40	0.84	4.47	87.16
Atlantic Mackerel *Scomber scombrus*	0.67	0.00	1.86	0.73	3.48	90.64

Table 4-2: SIMPER analysis results for the mouth of Placentia Bay vs the mouth of Conception Bay August 1998.

Average Dissimilarity = 65.76	**PB Mouth**	**CB Mouth**				
Species	**Average Abundance (/1000 m^3)**	**Average Abundance (/1000 m^3)**	**Average Dissimilarity**	**Dissimilarity/Standard Deviation**	**% Contribution**	**Cumulative %**
Capelin *Mallotis Villosus*	366.22	310.99	19.51	1.77	29.67	29.67
Cunner *Tautogolabrus adspersus*	178.32	176.19	14.69	1.45	22.35	52.02
Yellowtail Flounder *Limanda ferruginea*	0.23	8.89	7.27	0.87	11.06	63.07
Snail Fish *Liparis* sp.	0.55	4.48	5.22	0.94	7.94	71.01
Atlantic Cod *Gadus morhua*	9.23	0.09	4.42	0.97	6.72	77.73
Radiated Shanny *Ulvaria subbifurcata*	0.29	1.70	4.27	0.71	6.50	84.24
Four Beard Rockling Enchelyopus cimbrius	0.73	0.03	3.21	1.09	4.88	89.12
American Plaice *Hippoglossoides platessoides*	0.59	0.06	2.47	0.86	3.76	92.87

Table 4-3: SIMPER analysis results for Conception Bay head vs mouth of bay, August 1998.

Average Dissimilarity = 58.97	**CB Head**	**CB Mouth**				
Species	**Average Abundance (/1000 m^3)**	**Average Abundance (/1000 m^3)**	**Average Dissimilarity**	**Dissimilarity/Standard Deviation**	**% Contribution**	**Cumulative %**
Capelin *Mallotis Villosus*	176.23	310.99	18.03	1.77	30.58	30.58
Cunner *Tautogolabrus adspersus*	109.10	176.19	13.21	1.54	22.40	52.97
Yellowtail Flounder *Limanda ferruginea*	0.92	8.89	6.38	1.27	10.83	63.80
Radiated Shanny *Ulvaria subbifurcata*	2.46	1.70	5.67	1.30	9.61	73.41
Snail Fish sp. *Liparis sp.*	0.41	4.48	5.22	1.33	8.86	82.27
Atlantic Herring *Clupea harengus harengus*	0.11	0.54	2.06	0.67	3.50	85.76
Four Beard Rockling *Enchelyopus cimbrius*	0.65	0.03	1.90	0.64	3.22	88.99
American Plaice *Hippoglossoides platessoides*	0.10	0.06	1.84	0.72	3.12	92.11

Table 4-4: Mean species richness (SR), Shannon diversity (H'), and abundance (/1000m^3) shown for Conception and Placentia Bays spatial comparisons. P-values marked with an " * " indicate that values were calculated using non-parametric methods. Mean values were calculated using non-transformed data.

	Bay	**N**	**Mean**	**P-value**
Abundance	CB	36	300.08	0.001
	PB	45	787.61	
Richness	CB	36	5.42	0.134
	PB	45	6.40	
H'	CB	36	0.72	0.001*
	PB	45	0.48	

Table 4-5: SIMPER analysis results for Trinity and Fortune between Bay comparison, July 1982.

Average Dissimilarity = 70.21	**TB**	**FB**				
Species	**Average Abundance (/1000 m³)**	**Average Abundance (/1000 m³)**	**Average Dissimilarity**	**Dissimilarity/Standard Deviation**	**% Contribution**	**Cumulative %**
American Plaice *Hippoglossoides platessoides*	239.00	1.64	16.54	2.62	23.56	23.56
Atlantic Cod *Gadus morhua*	61.55	1.78	11.60	2.40	16.52	40.08
Capelin *Mallotus villosus*	1.00	31.77	6.51	1.02	9.28	49.35
Radiated Shanny *Ulvaria subbifurcata*	34.59	30.97	6.23	1.14	8.87	58.22
Redfish *Sebastes sp.*	10.85	29.30	6.22	1.15	8.86	67.08
Atlantic Herring *Clupea harengus*	53.39	10.77	5.46	0.93	7.77	74.85
Arctic Shanny *Sticchaeus punctatus*	9.08	0.03	4.40	0.86	6.27	81.12
Winter Flounder *Pseudopleuronectes americanus*	5.06	43.56	4.10	0.81	5.84	86.96
Snail Fish sp. *Liparis sp.*	6.80	2.19	3.97	0.95	5.66	92.62

Table 4-6: Mean species richness (SR), Shannon diversity (H'), and abundance (/1000m^3) shown for Trinity and Fortune Bays spatial comparisons. P-values marked with an " * " indicate that values were calculated using non-parametric methods. Mean values were calculated using non-transformed data.

	Bay	**N**	**Mean**	**P-value**
Abundance	TB	57	424.02	0.000
	FB	51	153.58	
Richness	TB	57	5.49	0.000
	FB	51	3.60	
H'	TB	57	1.02	0.210*
	FB	51	0.88	

Table 4-7: SIMPER analysis results for Trinity Bay and Conception Bay during June-August 1985.

Average dissimilarity = 71.72	TB	CB				
Species	Ave. Abundance	Ave. Abundance	Ave. Dissimilarity	Dissimilarity/Std. Deviation	% Contribution	Cumulative %
Capelin *Mallotus villosus*	521.10	248.08	10.99	1.16	15.32	15.32
Radiated Shanny *Ulvaria subbifurcata*	51.03	72.20	7.40	0.96	10.31	25.64
Cunner *Tautogolabrus adspersus*	40.75	327.62	7.31	1.04	10.20	35.83
American Plaice *Hippoglossoides platessoides*	33.60	39.36	7.16	0.80	9.98	45.82
Winter Flounder *Pseudopleuronectes americanus*	0.68	31.41	5.19	0.87	7.24	53.06
Atlantic Cod *Gadus morhua*	27.41	14.81	5.19	1.11	7.24	60.29
Whitch Flounder *Glyptocephalus cynoglossus*	65.01	43.19	5.12	0.92	7.14	67.44
Arctic Shanny *Sticchaeus punctatus*	24.19	3.14	4.65	0.51	6.48	73.92
Snail Fish Sp. *Liparis sp.*	8.44	8.85	4.56	0.77	6.35	80.27
Yellowtail Flounder *Limanda ferruginea*	1.38	52.33	3.96	0.84	5.52	85.79
Atlantic Herring *Clupea harengus*	2.76	9.52	1.95	0.49	2.72	88.51
Atlantic Mackerel *Scomber scombrus*	0.98	4.81	1.80	0.65	2.51	91.02

Table 4-8: SIMPER analysis results for Trinity Bay and Conception Bay during June-August 1986.

Average dissimilarity = 64.85	TB	CB				
Species	Ave. Abundance	Ave. Abundance	Ave. Dissimilarity	Dissimilarity/Std. Deviation	% Contribution	Cumulative %
Capelin *Mallotus villosus*	491.56	7189.77	10.61	1.09	16.36	16.36
Winter Flounder *Pseudopleuronectes americanus*	3.67	76.62	7.00	1.25	10.79	27.15
Snail Fish Sp. *Liparis sp.*	0.00	30.00	5.85	1.11	9.02	36.18
Radiated Shanny *Ulvaria subbifurcata*	11.89	52.86	5.73	1.05	8.84	45.02
Cunner *Tautogolabrus adspersus*	9.36	91.32	5.42	1.13	8.35	53.37
Whitch Flounder *Glyptocephalus cynoglossus*	16.04	45.08	4.85	1.15	7.47	60.84
American Plaice *Hippoglossoides platessoides*	36.85	51.28	4.64	1.14	7.16	68.00
Atlantic Cod *Gadus morhua*	10.46	23.66	4.41	1.21	6.80	74.80
Atlantic Herring *Clupea harengus*	4.26	64.99	4.14	0.99	6.39	81.19
Atlantic Snailfish *Liparis atlanticus*	6.24	0.00	2.93	0.90	4.51	85.70
Yellowtail Flounder *Limanda ferruginea*	1.18	16.82	2.81	0.91	4.34	90.04

V. Summary and General Conclusions

The three main elements that comprised this thesis were comparisons of different gears that are used for larval fish sampling, long-term temporal investigation of larval patterns, and a spatial investigation of larval fish communities in eastern Newfoundland embayments. The issue of addressing gear differences was essential to the other two elements because different studies have utilized different sampling approaches base on their objectives, whereas the data meta-analysis presented here requires that these data sets be considered in tandem. Many studies have investigated the changes in fish communities that occurred during the early 1990's when Atlantic groundfish collapsed (Helbig et al., 1992; Taggart et al., 1994; Gomes et al., 1995; Frank et al., 1996; Hutchings, 1996; Gerasimova and Kiseleva, 1998; deYoung et al., 1999; Rose et al., 2000; Rose, 2003; Rose 2004; Carscadden, 2005; Frank et al., 2005), however, the majority of these studies have focused on adult assemblages. This investigation represents an exploration of the long-term changes in composition that occurred within the larval fish community of eastern Newfoundland during the critical period surrounding the fisheries collapse in the early 1990s.

The sections below outline the goals and findings of this work for each of its three main components. As a final part of this chapter I suggest potential research directions to further some of the findings from this project.

i. Gear Comparisons

The objective of chapter 2 was to consider the potential bias issues that may be associated with the catalogue of ichthyoplankton data for the Newfoundland region because of the different sampling gears that have been used. Previously, there had been no attempts at gear calibration specific to ichthyoplankton communities in coastal Newfoundland, though much of the historical data has utilized either ring nets or bongo nets. The best opportunity to address such biases was to compare concurrent studies that utilized different gears. Data collected during the summers of 1985 and 1986 using bongo and ring nets were analyzed to determine whether estimates of abundance, diversity, and species richness of ichthyoplankton obtained by the two gears were inter-comparable and whether a consistent calibration factor could be developed.

Based on the comparisons carried out in this study, and the patterns in sampling bias that I was able to document for the purposes of the present study, that bongo and ring nets produce comparable estimates of Shannon-Wiener diversity, species richness, and abundance. In all of these instances, there is little doubt that the different gears contributed to sample variability, but the key finding is that this variability was inconsistent and thus added uncertainty rather than bias. Correction factors varied considerably in space and time, suggesting that no universal value could be applied and that no consistent bias in sampler efficiency could be identified. The variability in ichthyoplankton associated with different time periods was far greater than differences observed between samplers, and although analyses that combine the two types of samplers add additional sources of error, the error is small and the greatest concern is that it will make other effects more difficult to detect, which can lead to an increased potential

for Type II error. Thus, the absence of significant differences would be more difficult to interpret in this instance than effects that are significant.

The major obstacle that prevented more quantitative conclusions in this chapter was the absence of simultaneous collections of ichthyoplankton using Tucker trawls, bongo nets and ring nets. For future comparisons and for more precise interpretation of this data a calibration study that incorporates concurrent collections using the three gears as well as the different mesh sizes used in the historical collections would allow the calculation of precise calibration factors and the reduction of Type II error. The availability of such data would ensure that data collected in the future as well as past collections are readily available for quantitative assessment and interpretation. Nonetheless, the comparisons that were made allowed comparison across time periods and geographic areas with acknowledgement of the additional variability added by the different samplers.

ii. Long term temporal analysis

The goal of chapter 3 was to examine historical ichthyoplankton data sets in order to determine how these assemblages changed during the period surrounding the fisheries moratorium when significant changes in groundfish communities occurred. Because larval assemblages encompass a greater variety of species than commercial fisheries, and include species that are of limited vulnerability to these fisheries, they offer potential insights into the relative roles that overfishing and environmental variation have played in the changes that have occurred in fish communities in Newfoundland waters. Moreover,

ichthyoplankton surveys a greater array of taxa than adult fish surveys, including those conducted by scientists.

The analysis carried out in this chapter provided evidence that the diversity, abundance and richness of the larval communities within Trinity and Conception Bays changed during the collapse of groundfish in 1992. This study raised questions regarding the abundances and survival of larvae of commercially-targeted versus non-commercially targeted species and what role environment and fishing may have played in their declines. The results showed that in most cases, commercial and non-commercial species both showed lower average abundances after the 1990-1994 period relative to the previous decade. However, in the case of some non-commercial species, there was no decline or an increase in average abundance after this time whereas the opposite was true for many commercial species. Moreover, arctic cod was present in 1991 and 1994 samples but not in years before and after the period of collapse. Reports of lower than average water temperatures (Colbourne et al., 1997) during these same years suggests that further analysis that incorporates environmental data is necessary in order to make definitive conclusions regarding what aspects of the environment may have played a key role in re-structuring the larval community. Nonetheless, the apparent "recovery" in non-commercial taxa but not in commercial taxa is most parsimoniously explained by a more substantial impact of overfishing on groundfish. Thus, some aspect of environment contributed to changes in a wide range of species during the early 1990s but the effect was short term compared to the impact of overfishing on groundfish.

iii. Spatial analysis

The objective of chapter 4 was to determine whether temporal changes had occurred in species diversity or dominance of larval fish over a large (multi-bay) spatial scale (100's of km) during the previous two decades; a period when major changes occurred in commercial fisheries. Specifically, this study addressed whether changes in ichthyoplankton were analogous among the bays surrounding Newfoundland's Avalon Peninsula or whether changes in the larval fish community occurred primarily at a within-bay spatial scale. In other words is the variation within the bays greater or less than variation among the bays?

Analysis carried out in chapter 4 showed that temporal changes did occur in species diversity over a large spatial scale. Long-term changes in ichthyoplanton generally appeared to be analogous among the bays. Variations in community composition were shown at both the within-bay and between-bay scale. Bays located more closely in space appeared to have more similar species dominance. The analysis carried out here was not able to determine whether variation within bays or among bays was consistently greater. Concurrent collections within each of the individual bays would be extremely useful in making diversity comparisons. Further investigation into smaller-scale factors that may affect diversity, in addition to data collected more closely in time, are needed to make more conclusive arguments on scale dependence of larval fish diversity in this region. Greater understanding of the within-bay spatial patterns may allow more accurate predictions on spawning strategies and nursery grounds of individual species. Local

patterns provide a starting base for studies on large-scale interannual and seasonal variation, as well as changes related to overfishing.

Literature Cited

Carscadden, J.E. (2005) Did signals from seabirds indicate changes in capelin biology during the 1990s? - comment on Davoren & Montevecchi. Marine Ecology-Progress Series 285: 289-297.

Colbourne, E., B. deYoung, S. Narayanan and J. Helbig (1997) Comparison of hydrography and circulation on the Newfoundland Shelf during 1990-1993 with the long-term mean. Canadian Journal of Fisheries and Aquatic Sciences. 54 (Suppl.1): 68-80.

deYoung, B. R. Peterman, A.R. Dobell, E. Pinkerton, Y. Breton, A.T. Charles, M.J. Fogarty, G.R. Munro and C.T. Taggart (1999) Canadian marine fisheries in a changing and uncertain world. A report prepared for the Canadian Global Change Program of the Royal Society of Canada. Canadian Special Publication of Fisheries and Aquatic Sciences Number 129.199p.

Frank, K. T., J.E. Carscadden and J.E. Simon (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Canadian Journal of Fisheries and Aquatic Sciences. 53: 1473-1486.

Frank, K.T., B. Petrie, J.S. Choi and W. C. Leggett (2005) Trophic Cascades in a Formerly Cod-Dominated Ecosystem. Science. 308: 1621-1623.

Gerasimova, O.V. and V. M. Kiseleva (1998) Long-term Variations in Cod Distribution and Feeding on the Newfoundland Shelf in Spring and Summer. North Atlantic Fisheries Organization Science Council Studies. 31: 79–110.

Gomes, M.C., R.L.Haedrich and M.G. Villagarcia (1995) Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador shelf, north-west Atlantic, 1978-1991. Fisheries Oceanography. 4: 85-101.

Helbig, J, G. Mertz and P. Pepin (1992) Environmental influences on the recruitment of Newfoundland/Labrador cod. Fisheries Oceanography.1(1):39-56.

Hutchings, J.A. (1996) Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Canadian Journal of Fisheries and Aquatic Sciences 53: 943-962.

Rose, G. A., B. deYoung, D.W. Kulka, S.V. Goddard and G. L. Fletcher (2000) Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Can. J. Fish. Aquat. Sci. 57: 644-663.

Rose, G (2003) Fisheries Resources and Science in Newfoundland and Labrador: An Independent Assessment. Royal Commission on Renewing and Strengthening our Place in Canada. 84 pp.

Rose, G. A. (2004) Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. Can. J. Fish. Aquat. Sci. 61:1553-1557.

Taggart, C. T., J. Anderson, C. Bishop, E. Colbourne, J. Hutchings, G. Lilly, J. Morgan, E. Murphy, R. Myers, G. Rose, and P. Shelton (1994) Overview of cod stocks, Biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Marine Science Symposia. 198: 140-157.